

Long Calls Mediate Male-Male Competition in Bornean Orangutans:

an Approach Using Automated Acoustic Localization

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von

Brigitte Spillmann

von

Villnachern und Zofingen AG

Promotionskommission

Prof. Dr. Carel van Schaik (Leitung der Dissertation)

Prof. Dr. Marta Manser

Dr. Erik P. Willems

Dr. Maria A. van Noordwijk

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To my parents

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Thesis summary

Sexual selection theory explains the occurrence of traits that evolved to function in relation to mating behavior. These traits are divided into intra-sexual selection for traits that are advantageous in competition among same-sex individuals or inter-sexual selection for traits that make an individual more attractive to mating partners. Theory therefore predicts that the distribution of females in space - which serves to maximize access to resources and safety - is crucial for males' social strategies to get access to fertile mates. The extent to which a male can monopolize mating access to females strongly affects his competitive strategy, along the continuum of scramble and contest competition, with some interesting variations.

In this thesis I concentrate on the role of a sexually selected long-distance vocalization, the long call of Bornean flanged male orangutans (*Pongo pygmaeus wurmbii*) in intra-sexual competition. Orangutans are exceptional among non-human primates because of their semi-solitary social organization. All other primates are gregarious and live in mixed-sex groups, whereas the only other solitary species are nocturnal. Orangutans show a roving-male promiscuous mating system: females live alone in relatively small home ranges compared to males and (flanged) males roam and converge at, and compete for matings with, receptive females.

This social system is hard to observe for humans, which has made it hard to develop and test hypotheses about the nature of their intra-sexual competition mechanisms and the way individuals assess their relative fighting ability in respect to other rivals in an area. For this reason, I developed a passive acoustic localization system (ALS) that reveals male presence through their call activity in space and time. In chapter 1 I tested the utility and the validity of such a system for the long calls of the orangutans. This study (and all following studies) were conducted on data collected at Tuanan field site, Central Kalimantan, Indonesia. I installed an ALS in a grid of 300 ha, containing 20 autonomous time-synchronized recording devices placed in a regular lattice at 500 m intervals. The validated system consisted of following features: (i) reliable recognition of male long calls from sound files using a user-trained software algorithm that worked at distances up to 700 m from the nearest recorder, which resulted in a recording coverage

of approximately 900 ha; (ii) acoustic localization of calling males, which was accurate up to 200 m outside the microphone grid and thus resulted in a triangulation area of 450 ha. ALS is therefore a highly effective method to detect long calls and triangulate their position in a species where knowledge about male presence is difficult to capture. I also think that this method can also be advantageous for other highly vocal but scattered animals.

In chapter 2 I used the ALS data to develop and test hypotheses about the nature of male-male competition in Bornean orangutans with a roving male promiscuity mating system. I examined their sexually selected long-distance communication system to disentangle the mechanisms through which males compete over the access of matings. I found that a male's choice of an area was a function of the local fruit availability. Once there, the calling behavior was determined by the presence of sexually attractive females and the number of other flanged male in the area. These variables also predicted the response proportion and the proportion of males engaging in responding. Because of these results I concluded that intra-sexual competition mechanism in Bornean flanged males is a mix of scramble and contest competition. This mix is best summarized as confrontational assessment, where males increase their call rate to attract females and continuously update their dominance relations through commitment in long call interactions.

Since for certain research questions I needed not only the call occurrences in space and time but also the identity of the calling individuals (chapter 4) I validated in a next step (chapter 3) a method that enables to identify the long calls recorded through ALS. I used an automatic caller recognition algorithm to test the accuracy of acoustic long call identifications. I tested two datasets: the first consisted of high-quality recording taken during individual focal follows and the second consisted of long call recordings with variable microphone-caller distances from the ALS and therefore variable recording qualities. The software I used was originally developed for human speaker recognition (the MSR identity toolbox in Matlab). I found highly accurate identification with the high-quality recordings (93.3%, N=224 calls by 14 males) and with recordings stemming from ALS with variable microphone-caller distances (20-420 m): 72.3% correct identifications (N=123 calls by 10 males). These results show that automatic acoustic individual identification is possible with ALS data, although the accuracy declines with increasing distance due to signal degradation.

In chapter 4, I addressed questions about dominance in Bornean male orangutans. Dominance is usually dyadic and common measurements to estimate dominance relations reflect this. But in a species like the Bornean orangutan the social context is rather unstable. Males have to deal with new rivals or with rivals they have not met for a long time. Therefore, males have to assess their own fighting ability relative to rivals they rarely encounter but can rely on dyadic relationships with rivals they meet regularly. To capture this shifting social context I tested the hypothesis that long calls reflect contest motivation through individual's rates of long calling and responding to calls made by others. Individual flanged males increase their calling behavior in the presence of a highly valuable resource such as receptive females. This result confirms confrontational assessment on an individual level.

Additionally, we were able to show that long calls are not costly to produce and therefore do not support the assumption of a handicap signal. Hence, long calls rather act as conventional signals. Next, because uncertainty of rivals fighting ability is most pronounced in males that never met before or meet rarely, I predicted that competition involving visitor males is most intense. Indeed, I found that a relationship exists between the intensity of agonistic encounters (along the gradient from chase to fight) and the competing dyads' residence status. I also found that an individual's tendency to get involved in agonistic encounters is a function of his calling activity, i.e. his call rates and tendency to respond in a given time period. Finally, I was able to show that long call behavior depended on the condition of an individual. Males' call and response rates vary considerably across males over time. Losing and suffering injuries affected calling behavior of males after a fight. Additionally, fighting motivation as a measure of calling interactions predicted the outcome of agonistic encounters. Hence, even though the long call is a conventional signal that contains no production costs, individuals with enhanced calling and responding activity incur social costs, such as the risk of fights and injuries that serve to keep their calling behavior tightly related to their fighting motivation.

Zusammenfassung

Die sexuelle Selektion erklärt das Auftreten von Merkmalen, die entstanden sind, um das Paarungsverhalten zu regeln. Diese Merkmale werden in intrasexuelle und intersexuelle Selektion unterteilt. Intrasexuelle Selektion beschreibt Merkmale, die einen Vorteil im Konkurrenzverhalten zwischen gleichgeschlechtlichen Individuen mit sich bringen. Intersexuelle Selektion beschreibt Merkmale, die ein Individuum attraktiver als Paarungspartner machen. Um sich den Zugriff auf paarungsbereite Weibchen zu sichern, spielt die soziale Strategie der Männchen eine grosse Rolle. Diese ist jedoch, vor allem von der Verteilung der Weibchen im Gebiet abhängig. Die Verteilung der Weibchen in einem Gebiet dient vor allem der Maximierung des Zugangs zu Nahrungsressourcen und der Sicherheit. Daraus folgt, dass das Ausmass in welchem ein Männchen den Paarungszugriff monopolisieren kann seine Konkurrenzstrategie beeinflusst.

In meiner Doktorarbeit habe ich mich auf die Rolle einer sexuell selektierten Lautäusserung über lange Distanzen konzentriert, nämlich dem „long call“ der Orang-Utan Männchen (*Pongo pygmaeus wurmbii*). Dieser long call wird von den Männchen mit den auffälligen Backenwülsten und dem grossen Kehlsack produziert. Orang-Utans sind einzigartig unter den nicht-menschlichen Primaten, weil sie eine semi-einzelgängerische soziale Organisation zeigen. Alle anderen Primaten sind gesellig und leben in gemischt-geschlechtlichen Gruppen. Die einzigen anderen solitären Primatenarten sind nachtaktive. Orang-Utans zeigen ein promiskues Paarungssystem mit umherziehenden Männchen. Die Weibchen leben alleine in relativ kleinen „Streifgebieten“ im Vergleich zu den Männchen. Die Backenwulstmännchen streifen umher und konvergieren um fruchtbare Weibchen und dabei konkurrieren sie untereinander um Paarungen.

Dieses soziale System macht es schwierig systematische Beobachtungen anzustellen. Dies ist mit ein Grund, warum es schwierig ist Hypothesen zum Thema der intrasexuellen Konkurrenzmechanismen zu entwickeln und folglich auch die Art und Weise wie Individuen ihre relative Kampffähigkeit abschätzen, zu testen. Aus diesen Gründen habe ich mich für ein akustisches Lokalisationssystem (ALS) entschieden. Mit einem ALS können wir Anhand ihres Kommunikationssystems über weite Distanzen die Präsenz von Männchen in Raum und Zeit aufzeigen.

Im ersten Kapitel der Doktorarbeit habe ich die Umsetzung und die Validität eines solchen Systems (ALS) für die Long calls der Orang-Utans geprüft. Diese Studie (aber auch alle folgenden) wurde mit gesammelten Daten der Feldstation Tuanan, in Zentral Kalimantan, Indonesien durchgeführt. Ich platzierte 20 autonome, zeitsynchronisierte Rekorder in Abständen von 500 m in einer Rasteranordnung. Die Validierung des Systems erzielte folgende Erkenntnisse: (i) die Erkennung von Long calls in den aufgenommenen Dateien funktionierte gut mit einem benutzertrainierten Algorithmus bis zu Entfernungen von 700 m. Dies resultierte in einer akustische Abdeckung durch das Rekordersystem von 900 ha; (ii) die akustische Lokalisation von rufenden Männchen erzielte genaue Resultate in einem Lokalisationsgebiet welches 450 ha umfasste. Dieses Lokalisationsgebiet beinhaltet das ganze Rekorderraster zuzüglich eines erweiterten Einzugsbereichs von 200 m ausserhalb des Rekorderrasters. Ich bin sicher, dass diese Methode erhebliche Vorteile in der Erforschung anderer rufender und weit verstreuter Tierarten bringen kann.

Im zweiten Kapitel nutzte ich die mit dem ALS erhobenen Daten, um Hypothesen über die Natur der innermännlichen Konkurrenz in einem promisken Paarungssystem mit umherziehenden Männchen zu testen, nämlich jenes der Orang-Utans von Borneo. Um die Mechanismen des Konkurrenzverhaltens unter Männchen zu untersuchen, nutzte ich ihr Kommunikationssystem über weite Distanzen. Der zugrundeliegende Grund dieses Konkurrenzverhaltens ist Zugang zu Paarungspartnern zu etablieren. Ich fand heraus, dass Männchen nicht zufällig in bestimmte Gebiete wandern sondern, dass ihr Aufenthaltsort eine Funktion der lokalen Verfügbarkeit von Früchten war. Innerhalb soch eines Gebietes wurde ihr Rufverhalten von der Anzahl paarungsbereiter Weibchen und der Anzahl von Rivalen in diesem Gebiet bestimmt. Dieselben Variablen bestimmten auch die Proportion von Antworten auf Rufe anderer Männchen und die Proportion der Männchen, die überhaupt antworteten. Aufgrund dieser Resultate schloss ich darauf, dass der Mechanismus der intrasexuellen Konkurrenz bei den Backenwulstmännchen von Borneo eine Mischung aus „scramble“ (Resource wird erzwungenermassen geteilt) und „contest“ (um Resource wird gekämpft) Konkurrenz ist. Diese Mischung wird am besten mit „Konfrontationsbeurteilung“ beschrieben. Wobei Männchen ihre Rufrate erhöhen, um Weibchen anzuziehen und dabei kontinuierlich ihre Dominanzbeziehungen mit anderen Rivalen durch Rufinteraktionen aufdatieren.

Für gewisse Fragestellungen benötigte ich nicht nur Rufereignisse der Männchen in Raum und Zeit, sondern auch die Identität der rufenden Individuen (siehe Kapitel 4). Darum validierte ich in einem nächsten Schritt eine Methode, die es erlaubt von einem ALS aufgenommene long call Daten einem Männchen zuzuordnen. Dazu nutzte ich einen Algorithmus, der auf Individuen trainiert wurde und automatisch akustische Identifikationen anhand der Long calls macht. Hierfür testete ich zwei Datensätze. Der Erste bestand aus qualitativ hohen Aufnahmen aus kurzer Distanz, welche während dem direkten Beobachten von Individuen entstanden. Der Zweite bestand aus Long call Aufnahmen des ALS mit variablen Distanzen zwischen dem Mikrophon und des rufenden Männchens. Diese Variabilität der Aufnahmedistanzen hatte zur Folge dass auch die Aufnahmequalität variierte. Das benutzte Computerprogramm wurde ursprünglich für menschliche Sprechererkennung entwickelt (MSR identity toolbox in Matlab). Die Aufnahmen in hoher Qualität resultierten in 93.3 % (224 Rufe von 14 Männchen) korrekten Identifikationen. Die Aufnahmen des ALS mit variablen Distanzen zwischen Mikrophon und rufendem Männchen (20-420 m) erbrachten 72.23 % (123 Rufe von 10 Männchen) korrekte Identifikationen. Die Resultate zeigen, dass automatische akustische Identifikation von Orang-Utan Long calls mit den gesammelten Daten eines ALS möglich ist, auch wenn die Genauigkeit mit sich vergrößernder Distanz durch Signaldegradation abnimmt.

Kapitel 4 befasst sich mit Fragen der Dominanz von Orangutan Männchen. Dominanz ist im Allgemeinen dyadisch und die üblichen Messungen, die zur Analyse von Dominanz genutzt werden, zeigen dies auch. Jedoch hier untersuchen wir Orang-Utans von Borneo, deren sozialer Kontext sehr instabil ist. Männchen müssen sich immer wieder mit neuen Rivalen, oder mit Rivalen, die sie schon lange nicht mehr getroffen haben, auseinandersetzen. Daher müssen Männchen ihre eigene Kampffähigkeit, in Bezug auf die Rivalen, die sie selten treffen, immer wieder neu abschätzen. Mit Rivalen, die sie regelmässig treffen, können sie hingegen meist auf dyadische Dominanzbeziehungen vertrauen. Um diese stetigen Wechsel im sozialen Kontext einzufangen, testete ich die Hypothese, ob long calls die Motivation zu kämpfen widerspiegeln. Gemessen wurde das mit individuellen Rufraten und dem Antworten auf Rufe anderer Männchen. Backenwulstmännchen erhöhen ihr Rufverhalten, wenn eine wertvolle Resource, eben ein fruchtbares Weibchen im Gebiet anwesend war. Dieses Resultat bestätigte den Mechanismus der „Konfrontationsbeurteilung“ auch auf einer individuellen Ebene.

Zusätzlich konnten wir zeigen, dass long calls nicht teuer zu produzieren sind und daher die long calls die Annahmen für „Handikapsignale“ nicht erfüllen. Demzufolge agieren long calls eher als konventionelle Signale, die keine Produktionskosten aufweisen. Weil die Unsicherheit der Kampffähigkeit am grössten zwischen Männchen ist, die sich noch nie oder selten getroffen haben, formulierte ich die Voraussage, dass das Konkurrenzverhalten am intensivsten ist, wenn neue oder selten anwesende Männchen involviert sind. Tatsächlich fand ich eine Beziehung zwischen der Intensität von agonistischem Aufeinandertreffen (entlang des Gradienten vom Rivalen verjagen bis zum Kampf) und dem Residenzstatus der konkurrierenden Dyadenmitgliedern. Ich fand auch, dass die individuelle Neigung in agonistische Auseinandersetzung involviert zu sein, eine Funktion der Rufaktivität ist, z.B. die Rufrate und die Tendenz zu antworten eines Individuums in gewissen Zeitperioden. Schliesslich, war es mir möglich zu zeigen, dass das Rufverhalten von der Kondition eines Männchens abhängt. Die Ruf- und Antwortrate eines Männchens variiert zwischen Individuen und Zeitperioden. Das Verlieren eines Kampfes mit zugezogenen Verletzungen beeinflusste das Rufverhalten von Männchen. Zusätzlich konnte ich zeigen, dass Kampfmotivation als eine Messung von Rufinteraktionen, den Ausgang von agonistischem Aufeinandertreffen vorhersagt. Daher, obwohl der long call ein konventionelles Signal ist, nehmen Individuen mit erhöhter Ruf- und Antwortaktivität ein erhöhtes Risiko von sozialen Kosten in Kauf, wie z.B. das Risiko in einem Kampf verletzt zu werden. Daher scheint das Rufverhalten eng mit der Motivation zu kämpfen verknüpft sein.

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General Introduction

Aims of the thesis

With this thesis I aim to address questions about how widely dispersed flanged male Bornean orangutans compete for access to scattered females. Much of their competition is mediated by their long calls. Long calls are known to affect an individual's ranging behavior and regulate encounters between dispersed individuals (Delgado, 2003, Mitra Setia and van Schaik, 2007). Hence, because they mediate dominance relationships, we cannot understand male-male relationships without understanding this long-distance communication system. In this introduction, I will discuss the relevant theoretical concepts of communication biology and sexual selection, and background information about orangutan biology needed to understand the aims of the thesis.

Communication

When we discuss animal communication, and especially acoustic communication, some concepts need to be considered. Communication can occur through acoustic, visual, olfactory, and tactile modalities (Bradbury and Vehrencamp, 1998); signals can even be combined to become multimodal (Partan, 2002). Accordingly, communication occurs when a sender directs a signal in any modality to a receiver and influences its behavior (Bradbury and Vehrencamp, 1998). Maynard Smith and Harper (2003) defined a *signal* as “any act or structure which alters the behavior of other organisms, which evolved because of that effect, and which is effective because the receiver's response has also evolved”. Therefore, a signal has been shaped by selection but is not to be confounded with *cues* that may also provide information for a receiver but not with the purpose of information transfer (Bradbury and Vehrencamp, 1998).

Usually, communication systems do not consist of only a sender and a receiver. Therefore scientist adopted the term “communication network” to indicate the regular presence of non-intended receivers that can use the information conveyed by the sender through eavesdropping (McGregor, 1993, McGregor and Peake, 2000). In orangutans the long distance communication system may be a good candidate to consider eavesdropping because rival males and females may eavesdrop on acoustic call interactions between two males and gain information about the state of the interacting individuals (Spillmann et al., 2010). But the sender might also adjust its signaling to a receiver depending on the presence of additional receivers. This adjustment is controlled (voluntary control) and can therefore be seen as a strategic use of a signal. This use of a signal is referred to the audience effect (Slocombe and Zuberbuhler, 2007, Zuberbuhler, 2008).

Hence, a signal contains information that is broadcast by the sender. It has been shown in various studies that acoustic signals can reveal information about a caller's identity (Hammerschmidt and Todt, 1995, Mitani et al., 1996), its dominance status (Kitchen et al., 2003, Fischer et al., 2004, Neumann et al., 2010, Charlton et al., 2013), the context in which a call is given (Crockford and Boesch, 2003, Wich et al., 2003), or (in alarm calls) about predator class (Seyfarth et al., 1980) and urgency (Manser et al., 2002). In any context it is advantageous for a receiver to process the information obtained (Seyfarth and Cheney, 2003). Mathematically speaking, the information content of a signal is defined as a reduction of uncertainty it produces in the receiver, known as the Shannon information (Shannon, 1948). Accordingly, a signal should contain only the information that benefits the sender, and receivers should attend to it. This means that a predictable relation exists between a signal and an individual on one hand, and a specific social or ecological situation on the other, which allows a receiver to predict current states or upcoming events from attending to this signal (Seyfarth and Cheney, 2003, Seyfarth et al., 2010). In the case of intra-sexual competition, information about dominance status or identity improves an individual's assessment of its own fighting ability relative to rivals (Parker, 1974, Enquist and Leimar, 1987, Preuschoft and van Schaik, 2000). This view that signals broadcast information has major acceptance, but there is a minority that claim opposing ideas. They state that signals are always manipulative (Dawkins and Krebs, 1978), which was later translated by Owings and Morton (1998) into the proposition that a signal's structural features have a direct impact on a receiver's nervous system and therefore the response is a nervous system response triggered by these acoustic features. However, in this thesis we follow the idea that signals convey information (Seyfarth et al., 2010).

So far, I introduced the concept of acoustic signaling in the sense of information transfer but signaling in the physical sense needs to be considered because it has its limitations in sound transmission. Generally speaking, acoustic signals are voiceless or voiced sounds that are produced by a sender. A voiced sound means that the vocal cords are engaged in sound production and in voiceless sounds they are not; this can also be visualized in spectrograms where a voiceless sound does not show frequency bands but voiced sounds do. In a perfect system, a receiver should be able to extract the whole information content of the signal transmitted by the sender (e.g. identity, which can be reflected in the fundamental frequency and resonance frequencies). However, signal

propagation inevitably leads to information loss, and subsequent signal perception is therefore not always perfect (Bradbury and Vehrencamp, 1998). In physics sound is a vibration that propagates longitudinally as a mechanical wave through a medium such as air or water. Sound transmission is usually affected by: (i) the density and the pressure of a medium which affects the speed of the sound (e.g. air versus water); (ii) motions of the medium itself, which may increase or decrease speed of the sound (e.g. wind which can result in an up or down shift of the sound's frequency spectrum which is known as Doppler effect); (iii) viscosity of the medium, which determines the rate at which a sound is attenuated but is negligible in gas and air (Bradbury and Vehrencamp, 1998). Generally, sound intensity decreases with distance, and this loss of intensity is called *spreading loss* and results in ambient noise masking the signal. Ground attenuation, scattering and reverberation are other important sources of sound degradation during sound transmission (Richards and Wiley, 1980, Bradbury and Vehrencamp, 1998). Additionally, it matters whether sound is transmitted in an open field or in a forest habitat. Reverberation has more impact on sound degradation in forest habitats (Richards and Wiley, 1980, Waser and Brown, 1986, McGregor et al., 1997). This excursion into physics is important when we deal with acoustic signaling, notably when the study includes recordings of animal calls that are subsequently used in acoustic analysis (chapter 1 & 2).

Intra-sexual selection

A signal is the vehicle that transports information, but a signal is also embedded in a broader context. Accordingly, the study of animal communication is closely linked to the study of an animal's social system, and thus also addresses questions about social relationships, survival, and reproduction (Fichtel and Manser, 2010) (as well as questions about the evolution of human language, in particular the difference between human language and animal communication systems (Fitch, 2010). This thesis focuses on acoustic communication evolved through sexual selection where hypotheses are based on either inter-sexual (female mate choice) or intra-sexual processes (male mate competition). Hence the function of signals in this context is either to attract mates or to repel rival males, or both, as shown in the roars of red deer (Clutton-Brock and Albon, 1979, McComb, 1991).

Intra-sexual competition is directly linked to the distribution of females in space, and the males' ability to monopolize fertile females (Emlen and Oring, 1977, Kappeler and van Schaik, 2002). In the case of widely distributed solitary females, males can go for pair-

bonded association or roving over large areas in search of receptive females. We expect roving males that locate distributed receptive females when a male is not able to defend multiple females against rivals (van Schaik and Dunbar, 1990). When males rove, competition appears along a spectrum from scramble to contest. With scramble competition males are unable to monopolize fertile females. Hence, they try to find scarce and widely distributed fertile females before rivals do. The reproductive success depends on a male's ability to localize females and high sperm production is crucial (Schwagmeyer and Woontner, 1986, Andersson and Iwasa, 1996, Sigg and Goldizen, 2006). Hence, no male can monopolize reproduction and the prevalent mating system is low-skew polygynandry.

When mate-guarding males are able to monopolize fertile females and therefore contest competition pays off, contest competition is expected (Andersson and Iwasa, 1996). In this case, an important variable is whether males are familiar and thus have up to date social knowledge of each other's fighting ability. Where males are familiar to each other, clear-cut dominance hierarchies are expected where high-ranking males monopolize access to receptive females. Contest competition often comes along with sexual dimorphism and polygyny as in pinnipeds, where the dominant male is able to fully monopolize fertile females (Lindenfors et al., 2002). Where males are less familiar or knowledge of fighting ability must be updated regularly, acoustic communication plays an even more important role in intra-sexual competition. Here, we expect the calls to be honest signals of fighting ability, as shown in male elephants where males in musth contest each other through their "musth rumbles" (Poole, 1999).

Signals usually seem to be honest, especially when they are involved in reproductive competition, for if they were not, receivers would stop attending and responding to them, thus making them useless. The best-known signals in this respect are handicap signals (e.g. peacock tail an ornament), which are secondary sexual characteristics that convey information about male quality and function in mate attraction (Zahavi, 1975). The probably most famous example in mammalian species of honest signaling in the vocal domain is the roaring of the red deer (*Cervus elaphus*). Only high ranking individuals can bear the cost to produce relative long lasting and exhausting calls (Clutton-Brock and Albon, 1979, McComb, 1991). In non-human primates this honest signaling is found in the loud calls of baboons where listeners can assess the competitive ability by attending to the signal (*Papio cynocephalus ursinus*) (Kitchen et al., 2003, Fischer

et al., 2004). Theoretically, such signals could easily be faked by weak individuals in order to gain access to valuable resources but usually the production of such calls is costly or difficult to perform for them, either because of physiological costs (reduced immunocompetence because of elevated testosterone levels) or because of social costs (due to the risk of eliciting fights with rivals in better condition) (Grafen, 1990, Owens and Hartley, 1991, Johnstone and Norris, 1993, Silk et al., 2000, Mougeot et al., 2004). Therefore, honest signals provide receivers with accurate information about the signaler's relative fighting ability.

Intra-sexual competition mechanisms and assessment of a male's fighting ability in a roving male promiscuity mating system are an important part of this thesis. I examined these topics in Bornean orangutan males (*Pongo pygmaeus wurmbii*) which I introduce in the next paragraph before I turn to the short summary of the contents in the respective chapters of this thesis.

Orangutans

Orangutans are almost unique among primates in being diurnal and semi-solitary. Most primates are permanently gregarious and all other solitary non-human primates are nocturnal (Kappeler and van Schaik, 2002). Orangutans are highly sexually dimorphic, with flanged males almost twice the size of females (Rodman and Mitani, 1987) and they show extreme, irreversible male bimaturation, with two sexually mature male morphs: the larger flanged male and the unflanged male (Utami et al., 2002, Dunkel et al., 2013). Only the flanged males have secondary sexual characteristics such as cheek flanges, big laryngeal sacs, and a long-distance vocalization, the long call vocalization (Utami et al., 2002). Flanged males are generally dominant over unflanged males.

Their mating system is described as a male roving promiscuous mating system (van Schaik, 1996). Such systems with roaming males and scattered females are often found in a variety of mammalian species (Fisher and Lara, 1999, Derocher et al., 2010) but not in non-human primates that are usually permanently gregarious and live in mixed-sex groups. Differences between Sumatran (*Pongo abelii*) and Bornean orangutans (*Pongo pygmaeus*) lie in the difference of habitat productivity with Sumatran soils being more fertile and consequently generate higher plant productivity and fruit availability than Bornean soils (Marshall et al., 2009). This difference in habitat productivity leads to differences in the socio-ecology between Sumatran and Bornean orangutans where

Sumatran orangutans show higher degrees of sociability and gregariousness (Delgado and van Schaik, 2000, Mitra Setia et al., 2009, Utami et al., 2009a). Importantly, variation in their long-distance communication system is also reported (Delgado et al., 2009). For all studied populations a male spacing function of long calls is described where males adjust their spacing according calling rivals (MacKinnon. J, 1974, Galdikas, 1983, Mitani, 1985b). A mate attraction function is reported for Sumatran orangutans (Delgado, 2003, Mitra Setia and van Schaik, 2007), whereas in Bornean orangutans this function is less supported (Mitani, 1985a, but see Spillmann et al., 2010) and a female protection function through earshot-association seems to be altogether absent (Delgado, 2003, Mitra Setia and van Schaik, 2007, Spillmann et al., 2010).

Despite these tantalizing differences, overall very little is known about the underlying mechanisms of intra-sexual competition and the assessment of individual fighting ability through their long-distance signaling in this taxon. These kinds of research questions are difficult to address with data collected through individual focal follows of lone males because this information captures only a subset of the individuals present in an area and their interactions. For this reason, I planned and developed an acoustic localization system (ALS) – essentially a grid consisting of 20 autonomous recorders distributed in the study area over 300 ha – with the purpose to capture continuous data on individual male presence and orangutan long call occurrences in the study area (Chapter 1). This system records all long calls emitted in a well-defined area, and to identify the exact location from which each long call was given. Fortunately, an orangutan's long calls can be individually discriminated (Delgado, 2003, Lameira and Wich, 2008) and thus recognized by receivers and eavesdroppers, and also seem to contain information on the context in which they are emitted (Spillmann et al., 2010). My second methodological approach therefore was to establish an automated caller recognition procedure that was originally developed for human speaker recognition (chapter 3). These methodological innovations made it possible for the first time to conduct a detailed analysis of the flanged males' competitive strategies.

Contents of the thesis

This dissertation consists of four research chapters. Two chapters focus on methodological aspects; (i) extraction and localization of call occurrences with an ALS (chapter 1); (ii) validation of a caller recognition procedure to identify calling individuals

(chapter 3). Chapter 2 and 3 target male relationships. Chapter 2 examines male-male competition mechanisms reflected in male long calling behavior on a population level and concludes we are dealing with a system with an unstable contest competition mechanism defined as “confrontational assessment.” In the last chapter (chapter 4), I examine this phenomenon at the individual level, asking how individual males assess each other’s current fighting ability through their long-calling behavior (rates of calling, responses to other males’ calls).

Chapter 1: Validation of an acoustic localization system (ALS)

In the first chapter I aimed to validate the feasibility of an acoustic localization system (ALS) to examine the orangutan’s long distance communication system. I established an ALS to continuously record long call occurrences in the Tuanan study area in Central Kalimantan, Indonesia. I used 20 time-synchronized recorders with inter-microphone distances of 500 m. The recorders were continuously active during day time for 14 hours, from dawn to dusk. I collected acoustic data over 10 consecutive months, which resulted in around 9 Tb uncompressed acoustic data. Long call occurrences were extracted with a recognition algorithm trained with long call recordings (Agranat, 2009). These long calls were then assorted to long call events. I used then differences in the time of arrival at different records to localize call events in space (Wilson et al., 2013). I found that a recognition algorithm reliably detected long call events in the sound files until a maximum distance of 700 m. Next, I was able to show that even with a recorder grid of such large inter-microphone distances long call localization was accurate within the microphone grid, and in fact also in an additional rim outside of the grid, which resulted in a total area of 450 ha with accurate long call localization. These results demonstrate the feasibility of an ALS in a species with widely dispersed individuals. Thus, the combination of an ALS with conventional individual focal follow data should greatly facilitate efforts to obtain a complete picture of the social organization of Bornean orangutans.

Addition to chapter 1 automatization of the localization procedure

The most challenging part of the ALS was data management. This included signal extraction, where manual extraction was not possible just because of the immense data set 20 recorders x 14 hours = 280 hours of sound files in only one day. Subsequent data

analysis, in particular localizing orangutan long calls in space, would have been too time-consuming. Therefore, I started in collaboration with a software developer (Raphael Walker) to develop an automated approach. In particular this automatization includes: (i) data organization, (ii) editing of data, in particular a non-destructive approach to cut sound files in pieces that contain long calls, and assort them according to the call event they belong to, (iii) automated cross-correlation of sound files belonging to a call event to establish time of arrival differences, and (iv) localization of the caller's location using a maximum likelihood approach. The software applications were written in Python. All these aforementioned steps were automatized and after their completion only manual control was necessary. Nevertheless, even though the process was significantly accelerated, the whole procedure was still complicated because of the missing link to a database. Additionally, we are currently implementing the possibility to train recognition algorithms for call detection but also caller recognition through MFCC extraction (see chapter 4). Hence, we are still working on a database approach with implemented software applications. This allows for an easy handling of huge datasets but would also be beneficial for any other project of acoustic data analysis.

Chapter 2: Confrontational assessment as an intra-sexual competition mechanism in Bornean orangutans

In the second chapter we used the extracted long call data to examine the male-male competition mechanism in Bornean flanged males. Orangutan males range widely in search for scattered fertile females. Orangutan females do not broadcast their reproductive state as many other non-human primates do (Knott, 2001). Therefore, males can potentially choose a variety of competitive strategies. The long call, a sexually selected long-distance call (Delgado, 2006), was examined in order to disentangle the mechanisms through which flanged male orangutans may compete over mating access. Due to the differences between Bornean and Sumatran social systems (Delgado and van Schaik, 2000) I hypothesized that Bornean orangutan males' competition consists of a mix of scramble and contest competition, which contrasts with Sumatran orangutans, where preliminary evidence suggests stable contest competition (Delgado, 2003, Mitra Setia and van Schaik, 2007). I was able to address this question because of the ALS and the resulting comprehensive data about male presence and call activity in the area.

I found that male presence depended primarily on the local fruit availability. But a male's calling activity was mainly determined by the number of sexually attractive females and the number of males present in the area. Additionally, these same variables also predicted the proportion of calls a male responded to and the proportion of males that responded at all. The conclusion was that intra-sexual competition among Bornean flanged males comprises a combination of contest and scramble components, with increased advertising and assessment of rival's fighting ability when there are sexually attractive females present, which is best summarized as "confrontational assessment".

Chapter 3: Automated caller recognition procedure

In this chapter I validated a caller recognition approach originally developed for human speaker recognition. Orangutan flanged males' long calls contain information about identity, as shown in different studies (Delgado, 2003, Lameira and Wich, 2008, Spillmann et al., 2010), but an automated caller recognition approach has not been used so far. An automated and reliable approach is important because using an ALS does reveal the number of calls in an area and we can estimate the number of individuals present via a time-distance rule (a validated approach to discriminate individuals, see chapter 2), but the identity of a caller is usually unknown. Because I also wanted to use the ALS data to address how long calls mediate male-male relationships, individual identification is crucial. Therefore, I applied and validated the procedure of automatic individual identification using a mel-frequency cepstral coefficients (MFCC) feature extraction. This cepstral representation (MFCC) captures the vocal tract resonances, and is based on the source-filter model of human speak production (Davis and Mermelstein, 1980). These MFCC were modelled using a GMM-UBM framework (gaussian mixture model with universal background model) for their identification (Sadjadi et al., 2013). The UBM is a universal background model trained on a pool of data from a number of callers. We found that caller recognition worked reliably, yielding 93.3% correct identifications with high quality recordings, and 72.23% correct identification with recordings stemming from the ALS with variable microphone-caller distances (20 – 420 m). Therefore, caller recognition seems to be a valuable tool to extract caller identities in an ALS or in a passive acoustic monitoring in general.

Chapter 4: Long calls as indicators of contest motivation

In chapter 4, I examined whether long call rates and long call responses are indicators of a male's fighting motivation. In chapter 2 we had found that Bornean flanged male orangutans show confrontational assessment as their intra-sexual competition mechanism. Because flanged males roam widely in search for fertile females and even though some males are regularly present in a study area, others are not (Utami et al., 2009b). This continuous shifting of the social environment implies that individuals often deal with new rivals or rivals whose assessment is outdated. In such a situation where dyadic dominance relations are not reliable, assessment through an honest signal can be beneficial (Huntingford and Turner, 1987). However, long calls do not seem to be costly in terms of production (Delgado, 2006). Compared to ornaments or armaments acoustic signals used in competitive contexts vary over shorter time periods and are therefore more likely to convey information about short-term changes in motivation than fighting ability (Rubenstein and Hack, 1992, Vehrencamp, 2000). This suggests that orangutans, although they would benefit from having honest long-distance signals of fighting ability, do not have such a signal but rather a conventional signal used in intra-sexual competition that contains costs in the social domain (Delgado, 2006, Laidre and Johnstone, 2013).

An important question therefore is how males regulate their contest competition. I used data from the ALS over a 10-months-period. I found that (i) an individual's long call activity is a function of the presence of sexually attractive females as demonstrated in chapter 3 on a population level; (ii) that long call production is not costly; (iii) there is large variation in individuals' presence in an area, suggesting a division between resident males and visitors; (iv) that less familiar dyads (i.e. those involving non-resident males) were more likely to engage in high-intensity agonistic encounters; (v) that calling behavior is increased within individuals that commit in agonistic encounters; and (vi) that fighting motivation reflected in calling behavior varies considerably over time, and that injured males decrease their calling activity. Hence, a flanged male's long calling behavior, specifically long call rates and long call response tendency, reveals his fighting motivation. In conclusion, a male's decision to engage in potentially dangerous calling and responding behavior does depend on his condition and motivation.

Finally, I compared the feasibility to address such question with data from numerous day-long individual focal follows over a time period of 8 years and found that

without ALS, for most of the questions addressed above we would not have enough statistical power to answer them (see chapter 4). We can therefore conclude that ALS significantly improves our ability to identify male competition strategies.

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Chapter 1

Validation of an Acoustic Location System to monitor Bornean orangutan (*Pongo pygmaeus wurmbii*) long calls

Triangulation of an acoustic source

Brigitte Spillmann ¹, Maria A. van Noordwijk ¹, Erik Willems ¹, Tatang Mitra Setia ², Urs Wipfli ¹, Carel P. van Schaik ¹

¹ Anthropological Institute and Museum, University of Zurich, Zurich, Switzerland

² Fakultas Biologi, Universitas Nasional, Jakarta, Indonesia

Abstract

The long call is an important vocal communication signal in the widely dispersed, semi-solitary orangutan. Long calls affect individuals' ranging behavior and mediate social relationships and regulate encounters between dispersed individuals in a dense rainforest. The aim of this study was to test the utility of an Acoustic Location System (ALS) for recording and triangulating the loud calls of free-living primates. We developed and validated a data extraction protocol for an ALS used to record wild orangutan males' long calls at the Tuanan field site (Central Kalimantan). We installed an ALS in a grid of 300 ha, containing 20 SM2+ recorders placed in a regular lattice at 500 m intervals, to monitor the distribution of calling males in the area. The validated system had the following main features: (i) a user-trained software algorithm (Song Scope) that reliably recognized orangutan long calls from sound files at distances up to 700 m from the nearest recorder, resulting in a total area of approximately 900 ha that could be monitored continuously; (ii) acoustic location of calling males up to 200 m outside the microphone grid, which meant that within an area of approximately 450 ha, call locations could be calculated through triangulation. The mean accuracy was 58 m, an error that is modest relative to orangutan mobility and average inter-individual distances. We conclude that an ALS is a highly effective method for detecting long-distance calls of wild primates and triangulating their position. In combination with conventional individual focal follow data, an ALS can greatly improve our knowledge of orangutans' social organization, and is readily adaptable for studying other highly vocal animals.

Introduction

Remotely recorded animal vocalizations are useful in investigations of various research topics, including biodiversity assessment, species abundance, seasonality in communication, the effect of ambient noise or anthropogenic sounds, adaptations in signal directionality, or social networks (Blumstein et al., 2011). Additionally, some research questions require knowledge of the location of vocalizing animals. These requirements, namely identifying a call's occurrence both in time and in space, can be met by an Acoustic Location System (ALS) (McGregor et al., 1997). Although an ALS has many benefits (Blumstein et al., 2011, Mennill et al., 2012), its main limitation is that a signal's propagation capacity greatly determines inter-microphone distances. Because primate loud calls are well adapted for long-distance propagation, they are promising potential candidates for an ALS.

Acoustic tracking of vocalizing animals was originally developed for marine animals, especially cetaceans (Watkins and Schevill, 1972). More recently, studies of birds have increasingly come to use acoustic location to track individuals through their singing or calling to address different aspects of communication networks (Peake et al., 2001, Fitzsimmons et al., 2008, Foote et al., 2008, Lippold et al., 2008, Mennill and Vehrencamp, 2008). So far, acoustic tracking studies of terrestrial mammals are still scarce (Collier et al., 2010, Thompson et al., 2010, Wrege et al., 2012), and in particular there is no study of primates that combines acoustic location and behavioral data collection via observation. There is growing interest, however, in applying this technique to primates, especially to wild-living apes (chimpanzees and orangutans) where radio- or satellite-tracking are not possible (Piel, 2014).

For wild orangutans, direct focal observations provide only a very limited overview of their social system, especially on Borneo, where individuals - except for mother-offspring pairs - are usually solitary and widely dispersed. Direct encounters, especially between flanged males, are rare (Rijksen, 1978, MacKinnon, 1979, Galdikas, 1985, van Schaik, 1999, Mitra Setia et al., 2009). However, a conspicuous loud vocalization, the so-called "long call", given only by flanged male orangutans, often affects other individuals' (both males and females) ranging behavior and mediates social relationships (Galdikas, 1983, Mitani, 1985, Delgado, 2003, Spillmann et al., 2010). Long call production and duration are highly variable: flanged males tend to give long calls

several times each day and long calls last from 15 seconds to 4 minutes (Delgado et al., 2009). Additionally, van Schaik et al. (2013) showed that spontaneously given long calls announce future travel direction in Sumatran orangutans. The most effective observational approach – undertaking simultaneous individual focal follows – at best captures only a subset of the individuals and their interactions in a study area, and is logistically difficult. An ALS for long calls would provide a valuable complement to direct observations.

We studied Bornean orangutans in Tuanan, Central Kalimantan, a dense peat swamp forest with a dense orangutan population (4.25-4.5 individuals/km²) (van Schaik et al., 2005). We established an ALS to continuously record long call events in the study area, using 20 time-synchronized recorders placed in a lattice at 500 m intervals. The recorders were continuously active for 14 hours, from dawn to dusk. These time-synchronized recordings permit localizing long call occurrences through triangulation, via differences in the time of arrival of a signal at different recorders (McGregor et al., 1997, Mennill et al., 2006, Wilson et al., 2013). Moreover, because long calls are individually distinctive in their acoustic structure (Delgado, 2003, Lameira and Wich, 2008, Spillmann et al., 2010), we could identify the individuals that had emitted the recorded long calls, even if they were not directly observed. The advantage of an ALS is the standardized monitoring and detection of multiple individuals' calling behavior simultaneously. In combination with conventional focal follows, an ALS should lead to a better understanding of the flanged males' communication in time and space, as well as of the ranging responses of intended long call receivers and eavesdroppers.

The accuracy of triangulation depends on the density of microphones in an array, and is also affected by attenuation, scattering, and reverberation, more so in forest habitats than in open fields (McGregor et al., 1997, Mennill et al., 2012). We strove to reach a biologically meaningful compromise between covering a relative large area to get a broad picture of flanged-male abundance, ranging behavior and identity on the one hand, and maximizing the accuracy in localizing long calling males' positions and their corresponding ranging behavior on the other.

The aim of this study was to validate this orangutan ALS, in two main steps (Table I). In the first step we asked whether all long calls were picked up in the area of the ALS. We examined 25 recording days (around 350 recording hours) to verify whether a trained, automated recognition algorithm (Song Scope) reliably recognized independently verified long call occurrences. To estimate the actual area covered by the

microphone-grid, we examined the distances at which long calls are still reliably detected by a trained recognition algorithm.

In a second step, we checked whether the ALS correctly determined the locality of long calls. We established a validation procedure for the acoustic location measurements of 89 long calls given by seven flanged males who were followed by observers and whose GPS locations during long call events were therefore available for comparison. Spectrographic cross-correlation of signals from a pair of recorders aligns two spectrograms where the peak correlation value corresponds to the time of arrival difference of a signal at two recorders. With at least three recorders recording a long call, we could then use these pair-wise time-of-arrival differences of a signal to triangulate the location of a long calling male. Additionally, we examined the effect of distance from the microphone array, because several studies have reported that acoustic location accuracy degrades with increasing distance from the microphone array (McGregor et al., 1997, Mennill et al., 2012). The aim of this validation was to identify the area where an animal's position could be triangulated, and the area where the animals could be recorded but not triangulated. Additionally we wanted to explore the accuracy of this acoustic location method.

Table 1: Summary of the steps of the validation procedure

Step	Analysis	Validation
1	Locate long calls in sound files with a trained recognition algorithm. (Song Scope)	Does recognition algorithm locate all known long calls?
2a	Extraction of differences in time of arrival through cross-correlations. (Raven Pro 1.4)	
2b	Triangulation of long call position with different time of arrivals (Sound Finder)	Does Sound Finder provide correct locations for known LCs? Does the output error (ms) of Sound Finder correspond with distance to true location? Comparison of localization accuracy for LCs from inside versus outside the grid.

Methods

Study area and recording

Fieldwork took place at the Tuanan field station, Central Kalimantan, Indonesia (2.151° South; 114.374° East) from March 2012 until February 2013. The field site is part of the Mawas area, managed by a local non-governmental organization (Mawas) that aims to protect the rainforest from illegal logging, fires and poaching. The field site encompasses a 1,000 ha trail-system in a peat swamp forest that was previously selectively logged. The area is flat and forest structure is homogeneous (unpubl. data). Researchers and well trained long-term field assistants conducted individual focal follows according to standardized field methods (<http://www.aim.uzh.ch/Research/orangutannetwork/FieldGuidelines.html>). Whenever possible, we followed subjects from morning to night nest over a span of several days (6-10 days). Subjects included all age-sex classes. Using hand-held GPS devices (Garmin GPS 78), observers recorded GPS points every 30 min to indicate the position of the focal individual. Observers recorded additional GPS points whenever they heard a long call and, if the focal subject was a flanged male, whenever he emitted a long call. This research project adhered to the American Society of Primatologists (ASP) principles for the ethical treatment of non-human primates.

We placed twenty off-line, time-synchronized (via GPS), SM2+ (SM2 firmware 3.1.9) autonomous recording units in a lattice at 500 m intervals. The ALS thus encompassed a grid of 300 ha. Each recorder was equipped with a single omni-directional, weatherproof SMX-II microphone. A 12 V, 18 Ah dry gel battery, charged by a 20 Watt solar-panel on site, powered each SM2+ recorder, allowing it to run independently for about three weeks (H. Kühl, & O. Wagner, pers. comm.). In camp preparation of the power-systems (solar panel, solar charger, DCDC-converter, battery) and microphone wires for each recorder required approximately fourteen days, and installation of the recording grid in the forest approximately seven days (see supplementary material I chapter 1).

We settled on an average microphone density of 0.066 microphones/ha, which is extremely low compared with previous studies in which average microphone densities were about 10 microphones/ha (marmots: Collier et al., 2010, passerines: Wilson et al., 2013). Our microphone grid of 300 ha was correspondingly large. We chose this low

microphone density and large grid size for three reasons. First, long calls are audible up to ca. 1 km for human observers on the ground and are well adapted to long-distance propagation because of their acoustic structure, relatively low fundamental frequency, high sound pressure level (100 dB at 1 m), and high repetition of call elements (Mitani, 1985, Waser and Brown, 1986). Second, acoustic analysis can identify individual long-calling flanged males up to distances of 300 m from the microphone (Lameira and Wich, 2008). Third, a pilot study of re-recorded long call playbacks with distances up to 800-1000 m from the microphone showed that long calls are still identifiable as such in a spectrogram (unpublished results).

We placed microphones in trees at a height of ca. 10 meters, above the dense understory. A correspondence between the height of the microphone and the signaler should considerably improve receiving conditions (Dabelsteen, 2005, Mathevon et al., 2005, Maciej et al., 2011). For each recorder, the microphone hung down from a branch close to the tree's trunk and above the recorder's position. We used the mean of the GPS coordinates provided every 10 minutes by each SM2+ recorder (SD = 7 m) to define microphone positions. We set the sample rate at 22,050 Hz and sample size to 16-bit signed PCM. Continuous recording occurred from 04:30 until 18:30 (starting one hour before sunrise and ending one hour after sunset). Each recording file covered exactly 1h 57 mins, with a new file starting after a delay of three minutes. We staggered starting times of different recorders to ensure that at all times at least 15 of the 20 recorders were active. We saved the recorded files in a compressed .wac format without data loss and uploaded them every month from SD cards to an external hard drive.

Long call extraction

To search for long calls in the numerous .wac files, we established a trained recognition algorithm using Song Scope software with batch processing. Song Scope classification algorithms are based on Hidden Markov Models (HMMs) (Agranat, 2009). We established a long call recognition algorithm in three steps. First, we selected high-quality long call recordings of all flanged males that observers had recorded with a shotgun microphone (Sennheiser ME 67) during individual focal follows. We used this selection as a first training set to produce a "high quality recognition model". In a second step we incorporated long calls recorded by SM2+ of moderate quality (greater distance

between long call position and microphone) of different individuals into this model (see Buxton and Jones (2012)).

In the final step, we established optimal model parameters, including minimum frequency (200 Hz), frequency range (700 Hz), and sample rate (4000 Hz), based on the properties of long call acoustics. Additionally, we set Fast-Fourier Transform window size (512), FFT overlap (1/2), dynamic range ([20 dB] i.e., how much signal energy is used to compare call components; dB relative to peak call signal dB), maximum syllable duration (1,500 ms), maximum syllable interval (800 ms), and maximum song duration (60,000 ms).

Validation of extraction performance

We checked long calls identified by the trained recognition algorithm of Song Scope to remove false positive results (background noise or non-target calls). The sonogram allowed easy detection of false positive results which we subsequently discard from the spreadsheet (Buxton and Jones, 2012). Nevertheless, we calculated the false positive rate of the trained recognition algorithm. However, false negatives give much more insight into the accuracy of the trained recognition algorithm. To evaluate the success rate of Song Scope, we compared the success of Song Scope with known occurrences of “long calls” in the area, based on individual focal follows. We analyzed 25 recording days (350 recording hours of the ALS), during which we recorded 145 long calls with known time and location that were given by flanged male focal subjects. All follows took place in the recording area of our ALS. In total, the ALS recorded 981 long calls during these 25 days. Therefore, during individual focal follows of flanged males, human observers recorded 15 % of long calls given in the entire study area within this time period.

Area covered by microphone array

To assess the maximum distances at which recorders recorded long calls and the trained algorithm exclusively recognized them, we examined the probability of detection as a function of distance to the long call position from each of all 20 recorders. We excluded distances to non-active recorders. For this analysis we used 89 long calls given by seven focal flanged males. This procedure gave us an estimate of the area covered by our ALS outside the recorder grid (Fig. 4 in supplementary material II, chapter 1).

Time of arrival differences

To initiate the second step (triangulation of long call locality), we first converted compressed .wac files into .wav files with WAC2WAV Converter Utility 3.3.0 (Wildlife Acoustics), because Raven Pro 1.4 does not recognize .wac files. We subsequently down-sampled the .wav files from 22,048 to 6,000 Hz using WaveLab6 to reduce file size. This should not affect the results because a long call's fundamental frequency does not exceed 3000 Hz and the Niquist-Shannon sampling theorem states that a sampling rate is sufficient when the bandwidth of interest is half the sampling rate (Bradbury and Vehrencamp, 1998).

We established spectrographic cross-correlations to the time of arrival differences whenever at least three recorders recorded a long call. Spectrographic cross-correlation makes it possible to compare two spectrograms and align them according to the peak correlation coefficient (Fig. 1). The peak correlation coefficient corresponds to the time offset between the two spectrograms. We used a band-pass filter from 200-1000 Hz to remove background noise outside of the signal of interest. We set the window size to 256 samples with an overlap of 50% and window-type Hanning to generate fast fourier transformation (FFT), and normalized each audio file to 0 dB. Even though Raven Pro 1.4 generates correlation functions automatically, we manually inspected all of them, because the quality of the signal of interest was sometimes so low that Raven incorrectly assigned the highest cross-correlation. These differences in time of arrival of a long call recorded at different recorders were the basis of triangulating its position.

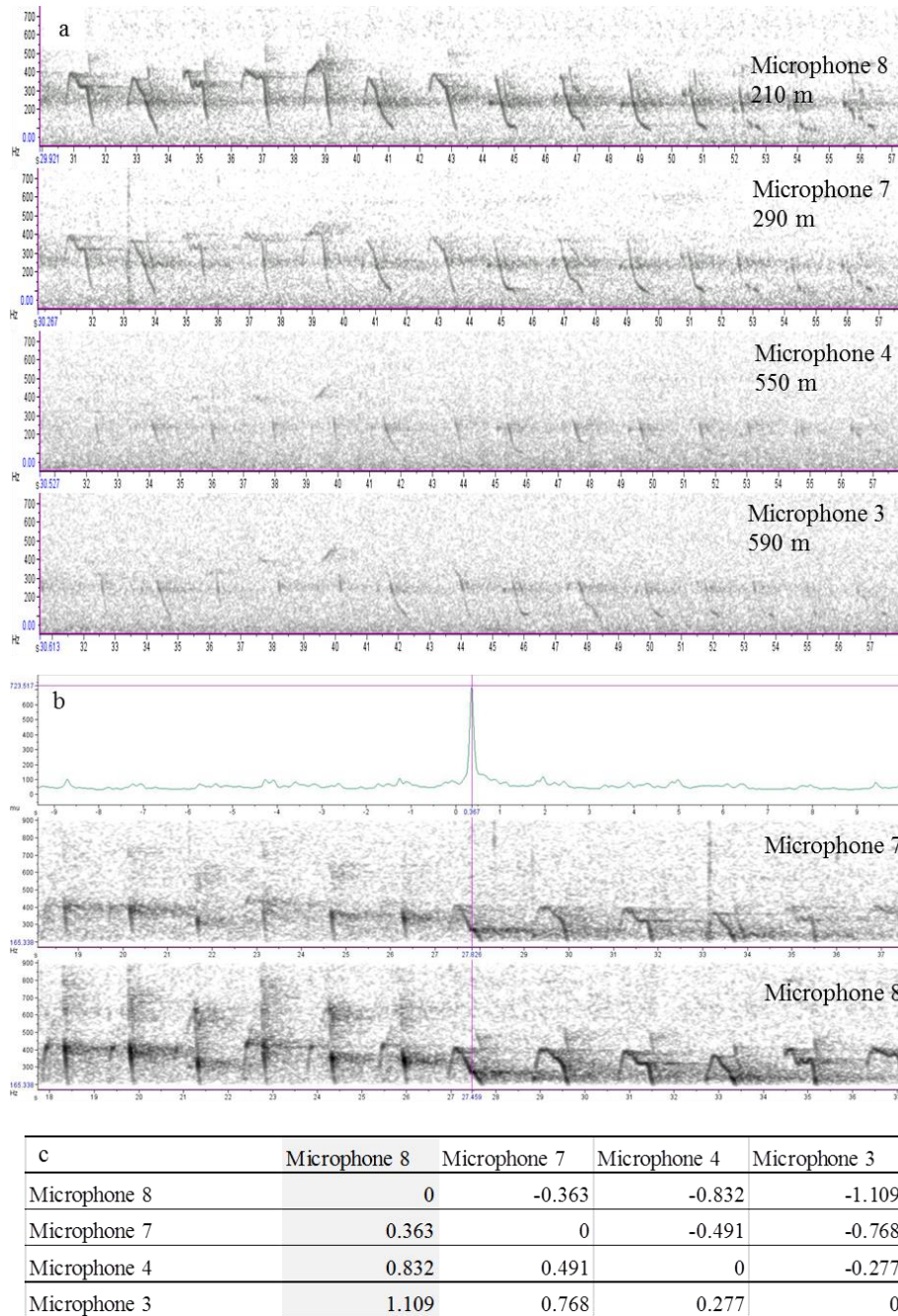


Figure 1: (a) Sonogram of a sequence of a long call recorded by four different microphones, (b) cross-correlation of two long calls with the peak correlation value that corresponds to the time of arrival difference, (c) results of peak correlation value between all recording files (see text).

Localization of long call source

We used Sound Finder a free available software developed by Wilson et al. (2013) to calculate the origin of a sound. It estimates the location of the sound source by applying the least-squares solution that was developed for global positioning systems. It also takes into account the temperature at the time of recording to calculate the corresponding

speed of sound. Although we used the mean hourly temperature in all subsequent analysis provided here, a comparison with results based on mean day temperature revealed a highly significant correlation between the two ($r = .99$, $t = 59.43$, $P < 0.001$). Moreover the difference in accuracy between these two approaches was not significant (Paired t-test: $t = -1.33$, $P = 0.188$, $df = 72$) indicating that future studies at Tuanan can also use mean day temperature, which is far easier to calculate. Note that this might be site-specific because of the small temperature fluctuation over the course of the day in a tropical forest habitat at low altitude.

We used Sound Finder to localize long call sources in two-dimensional space. The output of Sound Finder includes latitude and longitude of the long call's origin. Additionally, Sound Finder estimates the time it takes for a sound to travel to the closest recorder (measured in seconds) and an error associated with the localization (measured in milliseconds) where higher errors denote lower confidence in the accuracy of the localization (Wilson et al., 2013).

Validation of acoustic location

One factor that affects localization accuracy is the position of the sound source in relation to the microphone grid. The result of a triangulation is more reliable when the sound originates from within the area bounded by the microphones rather than from outside it (McGregor et al., 1997, Mennill et al., 2012). We therefore first concentrated on acoustic location results obtained for long calls originating within the microphone grid. We checked whether the error value produced by Sound Finder could be used to assess the accuracy of an acoustic location result. The accuracy of location was the distance in meters between the acoustic localization established by Sound Finder through triangulation and the corresponding GPS-position obtained by an observer who followed the calling male with a handheld GPS unit. It is important to note that coordinates measured with a handheld GPS unit have error margins of approximately 8 to 12 meters at Tuanan.

Using a Wilcoxon rank-sum test we then compared results obtained from triangulations within the area bounded by microphones versus results obtained from outside the microphone array. Acceptable Sound Finder errors never produced a localization error of >100 m. We therefore set the cut-off distance from the microphone

grid where triangulations became more inaccurate than those obtained inside the grid, at 200 m to stay within this acceptable localization error (Fig. 3).

This procedure allowed us to recognize three recording areas: in = inside the microphone grid, edge = up to 200 m outside the microphone grid, and out = >200 m outside the microphone grid. We conducted robustness tests (bootstrap with 9999 resamples) to assess whether these three areas differed according to the accuracy of triangulation results. All statistical tests were performed in R version 3.0.1 (R Core Team, 2015) and were 2-tailed.

Results

Success of recognition model

The success rate of the trained recognition algorithm using Song Scope was 99%: the recognition algorithm found 143 of 145 long calls observed during follows of flanged males. The two long calls that the trained recognition algorithm failed to recognize belonged to a flanged male with an exceptionally high-pitched voice (as had been obvious to human observers when naming him “Helium”) and in addition background noise masked one of these two long calls. The system did, however, recognize another 21 long calls (> 90%) by this same male. Thus, the algorithm recognized all “normal” long calls known to have been emitted from within the study grid. Every fourth annotation of the trained recognition algorithm noted a long call. Therefore, on average, 75% of the annotations were false positives. Despite these errors, the advantage of using an automated method over a manual method to recognize long calls is apparent, given that every month included an average of 21 recording days, resulting in approximately 5880 recording hours (20 recorders x 14 hours x 21 days).

Coverage area of ALS

The trained recognition algorithm recognized 77% of 89 long calls given by seven different flanged males at distances up to 600-700 m from a recorder (Fig. 2), including one long call that occurred at an exceptional distance of 1400 m. When we excluded “Helium” from this analysis, 87% of all long calls were still recognized at a distance of 600-

700 m. If two or more microphones were within this distance, the probability of the long call being detected by at least one was 98%. Therefore we can conclude that our ALS encompassed an area of approximately 700 m, outside of its own perimeter. This corresponds to a total area of around 900 ha covered by the microphone array (300 ha within the grid, and 600 ha outside).

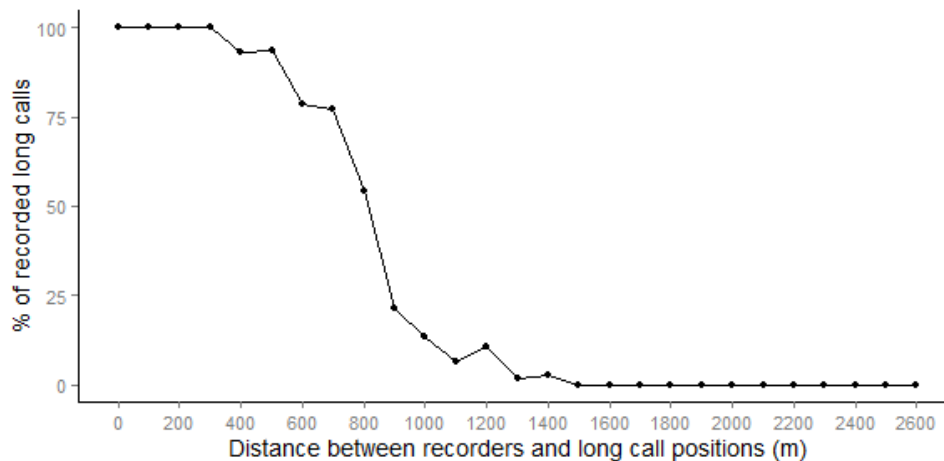
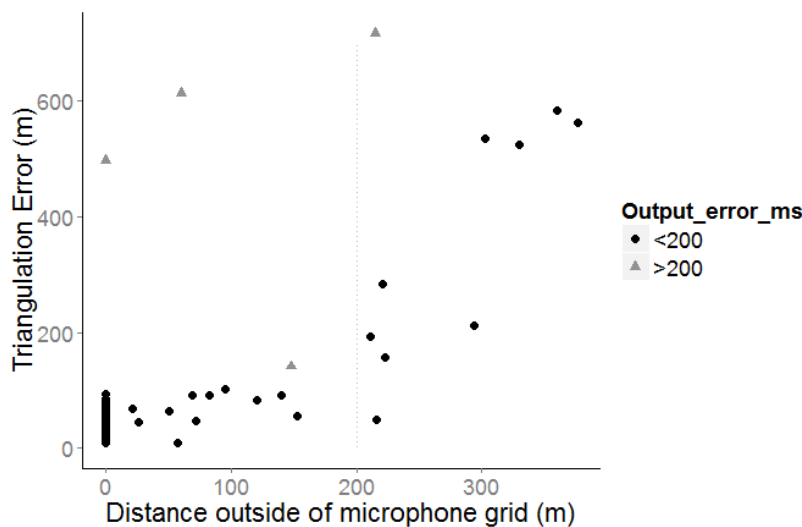


Figure 2: The effect of distance on the recognition success by the trained recognition algorithm of long calls in the sound files.

Triangulation: Localization of long calls with Sound Finder

Triangulations of 66 long calls that occurred in the area bounded by the recorders showed errors of 8-94 m (mean: $58 \pm \text{SEM } 7.2$ m; median: 50 m), with the exception of a single call, which yielded a deviation of 496 m from its actual location. These values were reasonable, if one takes into account that the directly observed location was also subject to error because of variable animal-human distance and the error of the handheld GPS unit. Sound Finder also reports the error in arrival times in milliseconds (ms). A perfect triangulation would produce an error of 0 ms. Therefore, because all acceptable long call triangulations showed an error value by Sound Finder <200 ms (the error of the failed triangulation was 2,000 ms), we included triangulations of long calls in the area bounded by the microphones and for which Sound Finder reported error values of <200 ms in our subsequent analysis.

To delineate how far the triangulation area extended outside the microphone grid, we also compared the triangulation accuracy of long calls given inside the grid (median error = 50.50 m) with long calls emanating from outside the grid (median error = 102.0 m), and found far greater triangulation errors for long calls occurring outside the area bounded by microphones (Wilcoxon signed-rank test, $Z = -4.60$, $W = 267.5$, $P = <0.001$, $N=89$).



were the same as those from inside the grid, whereas errors rapidly increased when calls emanated from farther outside the grid (Table II). We therefore used the 200 m extension of the microphone grid to delineate the triangulation area.

Table 2: Comparison of the accuracy of long call triangulations originating from different areas relative to the microphone grid

Comparison of different areas	Mean difference (m)	Bootstrap (9999 resamples)			
		Std. Error	p-value	Confidence interval 95%	
				lower	upper
in ¹ versus edge ²	-16.5	8.64	0.084	-32.6	1.4
in ¹ versus out ³	-293.4	68.64	0.016	-425.4	-162.2
edge ² versus out ³	-276.9	69.10	0.020	-408.7	-146.0

¹ long calls that occurred inside the microphone grid

² long calls that occurred < 200 m outside the microphone grid

³ long calls that occurred > 200 m outside the microphone grid

Discussion

We aimed to validate data extraction performance from an Acoustic Location System (ALS) set up to record the vocalizations of wild male Bornean orangutans. This validation showed (i) the reliable performance of the trained long-call recognition algorithm up to distances of 700 m, and (ii) the possibility to triangulate long call positions up to 200 m outside the microphone grid, with a mean triangulation error of 58 m.

Based on the results of this validation, we could divide the area that the ALS covered into (i) an area where acoustic location was possible up to 200 m outside the microphone grid, and (ii) a surrounding area, where only rough localization estimations were possible (see table III).

In this validation study, we did not attempt to identify the calling males in the acoustic landscape. However, Lameira and Wich (2008) showed that acoustic identification of long calls was possible up to a distance of 300 m from the sound source. Thus, individual identification should be possible within the triangulation area and might still be possible at distances between 300 m and 400 m (74% of the long calls fall within < 300 m, 91% fall within < 400 m of the closest microphone), given the much larger sample size of long calls that were recorded (via focal follows and the ALS) and consequently the far superior statistical power in the discriminant function analysis.

Table 3: Coverage of ALS divided into two areas

	Triangulation Area 450 ha	Recording Area 900 ha
All long calls recorded	yes	Prob. yes
Long call localization	yes	only rough estimate
Long call – ID ¹	yes	only presence of LCs
Use	ID + localization	No ID + rough localization, recognizing responses to LCs

¹ not yet verified*Factors that account for errors in the acoustic location results*

There are several explanations for the relatively high triangulation errors. First, sound propagation is affected by distance, leading to lower accuracy when distances between microphones are high. Second, localization accuracy is affected by habitat type: forest habitats lead to higher inaccuracy in acoustic location compared to open fields (McGregor et al., 1997, Bradbury and Vehrencamp, 1998, Andersson and McGregor, 1999, Mennill et al., 2012). One way to improve accuracy is to increase the height of the receiver (Dabelsteen, 2005). Therefore we installed microphones at a height of 10-15 m. Third, we defined triangulation error as the distance between the acoustic location of Sound Finder and the position of a corresponding long call recorded on a handheld GPS unit during an individual focal follow. At the Tuanan field site, handheld GPS devices show an error of approximately 8-12 meters, and observers take GPS points at ground level at a (horizontal) distance of ca. 5-20 meters from the focal subject. It is difficult to know the proportion of the triangulation errors caused by errors in the acoustic location established by the ALS vs. those that caused by GPS errors (error of GPS device and observer position relative to focal subject). Finally, rain and wind may affect the accuracy of results. Fortunately, long calls rarely occur during rain and especially not during hard rain. In the Tuanan population, observational data suggest that <5% of long calls occur during rain (unpubl. data). Strong wind conditions at Tuanan are rare and brief, usually occurring right before thunderstorms (pers. obs.). Moreover, closed habitats are generally less affected by atmospheric irregularities (Brown and Handford, 2000). Therefore, wind probably had only a minor effect on our results.

Is the acoustic location system accurate enough?

Although the localization errors of ca. 50 m may appear large, and certainly are large compared to other studies (McGregor et al., 1997, Mennill et al., 2012, Wilson et al., 2013), they are actually modest in relation to orangutans' mean inter-individual distances and daily mobility. Orangutans social organization is referred to as semi-solitary: individuals are widely dispersed, except for mother-infant pairs. Simultaneous follows of different sex-age classes in Suaq Balimbing revealed average distances between adult females and dominant or other flanged males of 550-730 m, and between flanged males and unflanged males of ca. 500 meters (Mitra Setia et al., 2009, Utami et al., 2009). In addition, mean daily travel distances of adult orangutans in Tuanan range from 700 – 900 m (unpubl. data). The farther away a conspecific's position to a long calling male, the smaller is the angle for a straight approach of this individual to the long call source. Thus, a triangulation error of 50 m on average - which accounts for 7-9% of the average inter-individual distances and 5-7% of the mean distance traveled by orangutans - has a minor effect on conclusions concerning ranging responses.

This study shows that an ALS, at this microphone density and number, is an effective tool to record and map all orangutan long-call occurrences in space and time in an area of 450-900 ha. One could argue that even at larger inter-microphone distances, viable results would be possible, but then microphone or recorder failure would have a much larger impact on data analysis. The ALS could enable us to monitor male presence in the study area as well as its ecological and social correlates. Therefore, several research questions can be addressed with the data acquired by the ALS. First, we will be able to track, over time and through space, the abundance of calling males in the area after identification is accomplished (in relation to ecological conditions and/or female reproductive state) as well as their ranging responses (male-male relationships). Second, we can monitor vocal responses to long calls by either focal flanged males or calling males recorded by the ALS (male-male relationships). Finally, we can use individual focal follows to document the ranging responses to long calling males by different sex-age classes (relationships between different sex-age classes). Thus, by combining an ALS with conventional individual focal follows, we can obtain a more complete picture of orangutan social organization.

While our study showed that an ALS works to detect orangutan long calls, we think that this method could easily apply to other primates emitting loud calls. This technology might especially enrich the study of species that are relatively difficult to observe or show a nocturnal lifestyle.

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Chapter 2

Confrontational assessment in the roving male promiscuity mating system of the Bornean orangutan

Brigitte Spillmann¹, Erik P. Willems¹, Maria A. van Noordwijk¹, Tatang Mitra Setia², Carel
P. van Schaik¹

¹Anthropological Institute and Museum, University of Zurich, Zurich, Switzerland

²Fakultas Biologi, Universitas Nasional, Jakarta, Indonesia

Abstract

In many solitary mammalian species, females live alone in relatively small home ranges whereas males roam widely and converge around, and compete for matings with, fertile females. In primates, orangutans are the only diurnal semi solitary species showing this roving male promiscuity mating system. Here, we develop and test hypotheses about the nature of male-male competition in Bornean orangutans by examining its sexually selected long-distance calls to disentangle the mechanisms through which males compete over mating access. This study uses a novel approach to disentangle the mechanisms of male-male competition. We established an acoustic localization system (ALS) comprising 20 recorders installed in a grid that allowed accurate localization in an area of 450 ha. With this procedure we triangulated 1615 long calls over 109 days spread over 10 months to examine the males' ranging and calling decisions. A male's choice of area was determined mainly by local fruit availability. Once there, however, his calling behavior depended primarily on the number of sexually attractive females and the number of other flanged males present. Both these variables also predicted the proportion of calls to which individual males responded, and the proportion of males present that responded to long calls of other males. We conclude that intra-sexual competition among Bornean flanged males comprises a combination of contest and scramble competition best summarized as confrontational assessment.

Introduction

According to socioecological theory (Emlen and Oring 1977; Kappeler and van Schaik 2002), the social strategies of females (resulting in a particular spatial distribution and social relationships) serve to maximize access to resources and safety, whereas those of males serve to maximize access to mates. Hence, males should distribute themselves according to female dispersion and compete over access to receptive females. The intensity and nature of this competition depend on details of intra-sexual selection (Emlen and Oring 1977; Clutton-Brock and Parker 1992; Arnold and Duvall, 1994; Andersson and Iwasa 1996). The aim of the present study is to examine the nature of male-male competition in a species with dispersed solitary females who experience rare and rather unpredictable receptivity and roaming males: the Bornean orangutan (*Pongo pygmaeus wurmbii*).

van Schaik and Dunbar (1990) suggested that where females are solitary and widely spaced, males can opt for pair-bonded association or roving over large areas in search of receptive females, with the optimal solution depending on his mobility relative to female territory size. If multiple females cannot effectively be defended against rival males, we expect a mating system with roving males that locate scattered receptive females. Such systems are indeed found in a variety of mammalian species (Fisher and Lara 1999; Andrès and Solignac 2003; Derocher et al. 2010).

Where males rove, one can discern a spectrum of male-male competition from scramble to contest. Scramble competition is expected when males try to find scarce, widely dispersed receptive females before rivals do, or cannot afford to remain in association with receptive females for long. In such a situation, the ability to localize females and high sperm production are crucial for a male's reproductive success (Schwagmeyer and Woontner 1986; Sigg and Goldizen 2006). Scramble competition is often reflected in a low-skew polygynandrous mating system where reproduction is not monopolized by a dominant male. In contrast, contest competition is expected when combat pays off because prolonged association is possible and guarding males can monopolize mating access. In situations in which males are familiar to each other, we expect clear-cut dominance hierarchies that mediate access to receptive females. Such absolute monopolization, accompanied by polygyny and elaborate sexual dimorphism, is known for pinnipeds (Lindenfors et al. 2002). Most commonly, however, some

intermediate situation will prevail because both sexes generally range alone and have insufficient information about each other's whereabouts and reproductive status. The resulting mating system is a form of high-skew polygynandry, where access is not fully monopolized by the top male because he is not necessarily the first male to locate the female (Dunbar 1988). Roving male mating systems usually are of this sort (Clutton-Brock 1989). The extent of male reproductive skew depends primarily on male mobility and density in relation to the density of receptive females (Dunbar 1988, 2000), but also on the interplay between male and female mating strategies, which may include female advertising of their reproductive status and male sexual coercion, in the form of forced copulations (Smuts and Smuts 1993), and post-copulatory mate guarding.

Orangutans are diurnal and semi-solitary, whereas most diurnal primates are permanently gregarious and all other solitary primate species are nocturnal (Kappeler and van Schaik 2002). Orangutans are highly sexually dimorphic with flanged males about twice as big as females (Rodman and Mitani 1987), and almost uniquely among mammals, they show extreme male bimaturism with two sexually mature morphs, the smaller unflanged and the larger flanged males. Only the latter have irreversible secondary sexual characteristics such as cheek flanges, big laryngeal sacs, and a vocalization, the long call (Utami et al. 2002). Orangutans show a roving male polygynandrous mating system, but because females show pronounced preferences for mating with (particular) flanged males (Utami et al. 2009a), in this study we concentrated on flanged males only.

Orangutan females are philopatric, with young females settling in home ranges overlapping with those of their mother, which enables them to maintain social relationships with their female maternal kin (Goossens et al. 2006; Arora et al. 2012; van Noordwijk et al. 2012). The size of female home ranges varies considerably across sites (Singleton et al. 2009; Utami et al. 2009b). Those of males are much harder to document, but the two available studies both report that flanged male home ranges exceed those of females in size by at least a factor 3-6 (Singleton and van Schaik 2001; Buckley 2014). Because of this and because female home ranges often show extensive overlap, each flanged male's home range overlaps with those of a considerable number of females. In addition, flanged male home ranges may be less stable, as suggested by the number of males recorded in the study area over time at our study site (see results). As a result, a large number of males may potentially compete over access to each receptive female.

The flanged male's long calls are known to repel male rivals and attract receptive females and can be heard up to 1000 m for human observers on the ground (Galdikas 1983; Mitani 1985a; Delgado, 2003, Mitra Setia and van Schaik, 2007). An additional function of long calls has been described for Sumatran orangutans, namely the female protection function. Non-receptive females try to maintain earshot association with the dominant long-calling flanged male in an area (Mitra Setia and van Schaik 2007), who has a smaller home range than the other flanged males (Singleton and van Schaik, 2001), which serves to avoid sexual harassment by other males and may perhaps also reduce the risk of infanticide (Delgado and van Schaik 2000; Fox 2002; Mitra Setia and van Schaik 2007). However, this protection function has so far not been found in Bornean orangutans (Mitani 1985a, b; Spillmann et al. 2010).

Because of their roving character, flanged males continuously need to decide where to go in order to find food and receptive females and how to behave toward other males. This behavior may depend largely on the number and identity of other males that are present and consequently reflect intra-sexual competition. Since long calls are a sexually selected signal (Delgado 2006), this long-distance communication system may reveal the nature of intra-sexual competition in male orangutans. Long calls can be assigned to individuals using measurements of the acoustic structure in combination with statistical methods (Delgado 2003; Spillmann et al. 2010) or with a caller recognition approach (Spillmann et al. 2016), and we therefore assume that male orangutans can identify each other by their calls.

Because none of the flanged males in the area are related to the local females (Arora et al. 2012), it is known that males leave their natal range and begin roaming. Given the larger size of the home ranges of flanged males compared to females, we expected the number of males recorded in the study area to increase for longer than the number of females.

Here, we make predictions as to how Bornean male orangutans adjust their local presence and long-calling activity in response to a variety of ecological and social factors to reveal what intra-sexual competition mechanisms are molding the system (see Table 1). We consider three basic cases: scramble competition, contest competition with stable dominance relations, and contest competition with unstable dominance relations. In the latter case, males must reassess their dyadic dominance status at frequent intervals,

perhaps at each encounter (if they have not met for a while). Sumatran males show stable contest competition (Singleton and van Schaik 2002; Delgado 2003; Mitra Setia and van Schaik 2007), but far less is known about Bornean males (see below), who are therefore the focus of this study.

I: Number of males

When receptive females are scarce and widely distributed and monopolization is prevented (e.g. because of high costs of association), scramble competition should prevail, and the number of males in an area should increase with the availability of receptive females. But if stable contest competition prevails, male presence in an area should not change or even decrease because subordinate males should avoid the dominant (see Table 1; cf. Singleton and van Schaik 2002). Under unstable contest, the number of males may increase or stay the same. In Bornean orangutans the mating skew among flanged males is found to be lower (Mitra Setia et al. 2009) and dominance relations among males more unstable (Galdikas 1983; H. Morrogh-Bernard et al. unpublished manuscript; BS unpublished data) than among Sumatran males. Thus, we predict an increase (which may be small or pronounced) in local male presence with the number of receptive females in the area.

II: Call rate

In a roving male promiscuity mating system the expectation is that long call activity should increase as a function of the availability of receptive females. Males need to advertise themselves in order to attract females. This outcome might reflect either scramble competition where males confront each other or unstable contest competition where dominance relations are reassessed at each encounter. On the other hand, under stable contest competition, no relationship should be found or even a decrease in long call activity because only males with higher relative dominance or greater fighting ability are able to increase their call rate and take the risk, whereas males with lower relative dominance or fighting ability will avoid dominant males or reduce their call rate or even stop calling when faced with more dominant rivals (Table 1; cf. Delgado 2003; Mitra Setia and van Schaik 2007). Because of the unclear dominance relations among Bornean males, we predict no change or an increase in male calling rate when receptive females are present.

III a and b: Long call response tendency and the proportion of responding males

Reactions to long calls, both how likely a male is to respond and whether he responds at all (i.e. the proportion of males present that respond to other males' calls) may provide the greatest resolution in disentangling the nature of male-male competition among Bornean orangutans. Assuming scramble competition, the presence of fertile females or other males should not affect the proportion of emitted long call responses, nor, as a consequence, the proportion of contributing males. In the case of stable contest, both the proportion of long call responses and the proportion of contributing males should decrease with both the number of sexually attractive females and the number of males present in the area. However, in unstable contest we expect the opposite: long call response probability and the proportion of responding males should increase with both the number of sexually attractive females and the number of males present in the area (see Table 1). There is no relevant information on Sumatran males.

Apart from these social factors, ecological factors such as fruit availability and rainfall may also have an effect on calling activity. First, earlier studies reported that fruit availability had no effect on long call activity in Sumatran orangutans (Delgado 2003), suggesting that the energetic costs of long call production are low. However, Bornean habitats show lower overall productivity and higher seasonal variation of fruit availability (Wich et al. 2011; Vogel et al. 2015), which might lead to energetic constraints on long call production, at least during certain time periods. Second, rainfall might have a more direct effect on long call production since sound propagation is highly affected by rainfall (Wiley and Richards 1982). Its effects have so far not been examined, but because males can also call between rain showers, we do not expect this to affect daily rates of long calling.

In traditional observational field studies in a limited study area it is very difficult to test the predictions derived above (Table 1), because it is impossible to collect accurate information on local male presence. We therefore adopted a novel approach using an automated acoustic localization system (ALS) that allowed us to gather continuous long call data from a recorder grid that encompassed an area of accurate acoustic localization of 450 ha (henceforth called triangulation area) (Spillmann et al. 2015). In this study we used the data extracted from the triangulation area so as to obtain an accurate estimate of the number of flanged males present in it.

Table 1 Predictions as a function of the number of sexually attractive females for (I) the number of males present in an area; (II) for average individual long call rate (III a) for the proportion of responding males and (III b) the proportion of long call responses

Dependent variable	Condition	Predictions as a function of the number of sexually attractive females
I: number of males	stable contest	decrease of male presence or no changes
	unstable contest	increase of male presence
	scramble	
II: long call rate	stable contest	decrease of long call rate or no changes
	unstable contest	increase of long call rate
	scramble	
III a: response proportion	scramble	no change in the response proportion
	stable contest	response proportion decreases or no changes
	unstable contest	increase of response proportion
III b: proportion of responding males	scramble	no change in the proportion of responding males
	stable contest	proportion of responding males decreases or no changes
	unstable contest	increase of the proportion of responding males

Methods

Study area

Field work was conducted at the Tuanan field station in Central Kalimantan, Indonesia (2.151° South; 114.374° East) from March 2012 until December 2012. The field site is part of the larger Mawas conservation area and covers a 1,000 ha trail-system in a peat swamp forest that had undergone selective logging around 20 years earlier. An advantage of swamp forests is the absence of topographic barriers for sound transmission. Researchers and long-term field assistants performed individual focal follows according to a highly standardized field protocol (see: <http://www.aim.uzh.ch/Research/orangutannetwork/FieldGuidelines.html>). In analyses where data of focal follow sampling was used, we included only focal follows lasting > 5 h. The ALS data were automatically recorded and analyzed and therefore blind. As to the behavioral data, it was not possible to record data blind because our study involved focal animals; however, none of the observers were aware of the hypothesis we were testing. This research project adhered to the American Society of Primatologists (ASP) principles for the ethical treatment of non-human primates.

Male roving behavior

We compiled data on newly identified individuals, in particular adult females and flanged males, from 2003 – 2014.

Data from the acoustic localization system (ALS)

We installed an acoustic localization system (ALS) consisting of 20 off-line, time-synchronized (via GPS), SM2+ autonomous recording units in a lattice at 500 m intervals, thus encompassing an area of 300 ha. The ALS was programmed to record continuously from 04:30 to 18:30 local time, to cover the orangutan's entire diurnal activity period. In total, we recorded and localized 3018 long call occurrences on 109 days, spread out over a period of 10 months (March 2012 – December 2012). To validate our automated acoustic localization algorithm, we used data from days during the study period on which flanged males were directly observed, either during individual focal follows or when in association with a female focal individual. This revealed a mean localization error of 58 m (SEM = +/- 7.2 m) for long calls occurring within the recorder grid, as well as within a peripheral area spanning up to 200 m outside of the grid, covering a total triangulation area of 450 ha. Given that localization accuracy outside of this triangulation area was lower, we restricted our analyses to only consider long calls occurring within the triangulation area (N= 1615). For more details on long call extraction and localization, see Spillmann et al. (2015).

One critical assumption we make for using the ALS method as a proxy of male presence is that each flanged male calls at least once per day while present in the study area. We validated this assumption with focal follow data which showed that males indeed called on 93.8 % of observational days (more details see supplemental I, chapter 2). Therefore, the ALS provides a highly accurate (minimum) estimate of the number of flanged males present within the study area at any day.

Ecological factors

Monthly fruit availability was determined by means of a standardized phenological protocol (<http://www.aim.uzh.ch/Research/orangutannetwork/FieldGuidelines.html>) for ~1500 trees in a 2 ha plot. From these data, a monthly fruit availability index (FAI) is

calculated, which is defined as the *number of trees carrying fruit / total number of trees monitored*.

During focal follows, flanged males were rarely observed to give long calls during heavy rain, and we found that hourly long call rates were significantly lower during rain showers (Median = 0.0) than during dry periods (Median = 0.633; Wilcoxon rank sum test: $W = 98$, $P < 0.013$, $r = -0.552$). The day's total rainfall was therefore measured locally, and included in all statistical models.

Number of males in the study area

Because we are not yet able to reliably assign each individual long call to a particular male, we used a validated approach to count the number of males in the area. For this, we used a two-component procedure. First, six of the males could typically be identified by idiosyncratic structures in the spectrograms of their long calls. Second, we applied a time-distance rule that assigned two calls to the same male if they occurred within 4 hours and a 300 m radius from each other under the additional restriction that speed of movement did not exceed 550 m/h. This rule was derived empirically from long call data from focal animal sampling over the course of complete follow days ($N_{\text{total LCs}}=848$ ($N_{\text{focal LCs}} = 242$, $N_{\text{others LCs}} = 606$), 96.8 % correct assignments, false pos. = 10, false neg. = 17). This procedure, when complemented with focal follows and additional sightings, allowed us to assign 1615 of the long calls to individual males.

Average long call rate per male

The average long call rate per male was estimated as the total number of long calls given per day divided by the total number of males in the area, as calculated above.

Proportion of long call responses and of responders

We defined responses as any long call that occurs within 5 minutes at a distance <1300 m of a prior long call given by a different flanged male. We exclusively focused on immediate call responses (<5 min) to capture highly competitive vocal exchanges and omitted responses with longer latencies ($5 < \text{latency} < 18$ min; supplementary material II, chapter

2, Fig. 1). The cut-off distance of 1300 m was chosen, given that distance had no effect on immediate long call responses until this distance. We also calculated a second measure, namely the proportion of responding males among the total number of calling males in the area per day.

Number of sexually attractive females

Unlike chimpanzees and bonobos, orangutan females do not indicate the peri-ovulatory period through sexual swellings (Galdikas 1981). In order to establish the conception time of a female we calculated 8.5 months back from known or estimated dates of birth of offspring (Graham 1988). A female was taken to be sexually active up to 6 months before, and 2 months after the time of estimated conception, based on patterns in mating activity (L. Dunkel, unpublished data). Using this criterion, two sexually attractive females were identified during the entire observation period, with a slight overlap in their respective periods of sexual attractiveness.

Statistical analysis

Model I: To predict the number of males within the study area at a given day, we fitted a generalized linear model (GLM) with a Poisson error distribution, incorporating the number of sexually attractive females present, fruit availability, and total rainfall as main predictor variables. Next, we fitted a series of models to assess which social (number of males and number of sexually attractive females present) or ecological (monthly fruit availability and total rainfall) variables (fixed effects) best predicted the following aspects of long call activity within our study area: Model II for the call rate per male per day (linear model, LM), Model IIIa for the proportion of long calls produced as a response to a preceding long call (binomial GLM), and Model IIIb for the proportion of males that responded to the calls of other males (binomial GLM). In all models, the interaction between the number of males and the number of sexually attractive females was considered, but this never reached statistical significance and was therefore omitted from the models reported here. The likelihood ratio tests were done by comparing all variables of each model with the null model. Where required, data were transformed prior to

analyses, and all models were conducted in R3.1.3 (R Core Team 2015) using packages “car” and “MuMIn”(Fox and Weissberg 2011; Barton 2016).

Results

Male roving behavior

New flanged males did indeed continue to enter the study area (Fig. 1), whereas the number of females remained roughly constant, apart from a sudden increase in 2007-2008, caused by the increase of the study area from 700 to 1000 ha during this time period, and local female recruitment due to maturation. Moreover, because some of the new males were clearly quite old, male ranges may also be far less stable than those of females. This pattern confirms that we are indeed dealing with a roving male mating system.

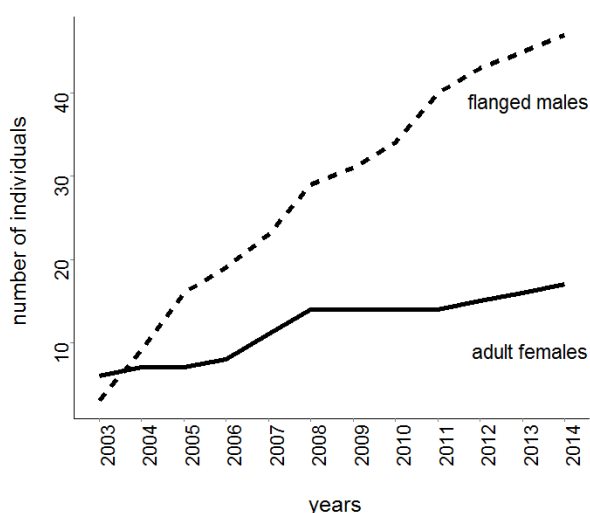


Figure 1: Cumulative counts of identified individuals over the years at Tuanan field site

I: Social and ecological correlates of male presence

In our first model we tested which factors account for the number of males present in the area. A significant Poisson GLM ($\chi^2_{LRT} = 30.084$, $R^2_{GLM(c)} = 0.036$, $P < 0.001$, $N = 109$) led us to reject our prediction that the number of sexually attractive females would affect male presence (see Table 2). Only fruit availability had a significant and positive effect on male presence in the area ($B = 0.087$, $SE = 0.019$, $t\text{-value} = 4.557$, $P < 0.001$).

Table 2: The effect of food availability, rain, and the number of sexually attractive females on the number of calling males in the area of 109 days spread over a 10-month period. Parameter estimates, associated standard errors and statistical significance as obtained from a poisson GLM

Fixed effects	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	1.084	0.097	11.188	
Ecological factors				
Food availability	0.087	0.019	4.557	<0.001
Rain	-0.004	0.004	-1.106	0.269
Social factors				
nr. of attractive females	-0.003	0.093	-0.034	0.973

$\chi^2_{LRT} = 30.084$, $p < 0.001$

II: Average long call rate per male

Using a linear model ($\chi^2_{LRT} = 4.05$, $R^2_{LM(c)} = 0.285$, $P < 0.001$, $N = 109$), we found that the average long call rate of a male present in the study area was a function of the number of sexually attractive females ($B=0.204$, $SE=0.06$, $t\text{-value}=3.423$, $P < 0.001$), as well as the number of other males in the area ($B=0.054$, $SE=0.024$, $t\text{-value}=2.298$, $P = 0.024$) (see Fig. 2 and Table 3).

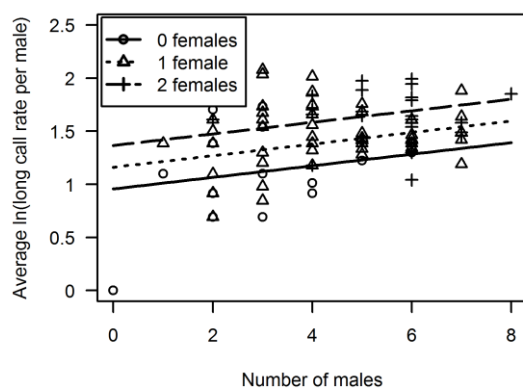


Figure 2: Probability of average individual $\ln(\text{long call rate per day})$ as a function of the number of sexually attractive females and the number of males present in the area. Prediction lines were obtained from a linear model. Data points represent the raw data.

Table 3: The effect of food availability, rainfall, the number of sexually attractive females, and the number of males in the area on the average individual call rate per day of 109 days spread over a 10-month period. Parameter estimates, associated standard errors and statistical significance as obtained from a linear model with $\ln(\text{long call rate per day})$

Fixed effects	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	0.985	0.087	11.328	
Ecological factors				
Food availability	-0.006	0.017	-0.360	0.719
Rain	-0.001	0.002	-0.312	0.756
Social factors				
nr. of attractive females	0.204	0.060	3.423	<0.001
nr. of flanged males	0.054	0.024	2.298	0.024

$\chi^2_{\text{LRT}} = 4.05, p < 0.001$

III: Long call interactions

III a: Proportion of long call responses

A binomial GLM ($\chi^2_{\text{LRT}} = 33.687$, $R^2_{\text{GLM(c)}} = 0.087$, $P < 0.001$, $N = 109$) found that the tendency to immediately respond to the long call of another male was largely explained by the number of attractive females currently present ($B=0.676$, $SE=0.182$, $t\text{-value}=3.713$, $P < 0.001$), as well as the number of flanged males in the area ($B=0.255$, $SE=0.086$, $t\text{-value}=2.976$, $P = 0.003$), while neither fruit availability nor rainfall had an effect (see Fig. 3 and Table 4).

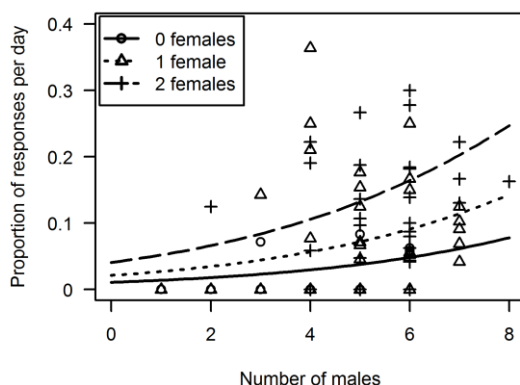


Figure 3: Probability of the proportion of long calls that elicited responses on a given day in the area as a function of the number of males in the area and the number of sexually attractive females. The prediction lines refer to the binomial GLM predictions

Table 4: The effect of food availability, rainfall, the number of sexually attractive females, and the number of males in the area on the proportion of long call responses of 109 days spread over a 10-month period. Parameter estimates, associated standard errors and statistical significance as obtained from a binomial GLM

Fixed effects	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-4.157	0.426	-9.749	< 2e-16
Ecological factors				
Food availability	-0.064	0.044	-1.455	0.146
Rain	-0.015	0.010	-1.608	0.108
Social factors				
nr. of attractive females	0.676	0.182	3.713	<0.001
nr. of flanged males	0.255	0.086	2.976	0.003

$\chi^2_{LRT} = 38.687$, $p < 0.001$

III b: Proportion of responding males

A binomial GLM ($\chi^2_{LRT} = 48.546$, $R^2_{GLM(c)} = 0.188$, $P < 0.001$, $N = 109$) showed that the proportion of responding males increased with the number of sexually attractive females ($B = 0.657$, $SE = 0.230$, $t\text{-value} = 2.856$, $P = 0.004$) and the number of males present ($B = 0.336$, $SE = 0.114$, $t\text{-value} = 2.946$, $P = 0.003$) (see Fig. 4 and Table 5). This indicates the presence of a crowding effect, but also that a greater proportion of the males present commit to calling when sexually attractive females are present. Again, neither fruit availability nor rainfall were significant predictors in the model.

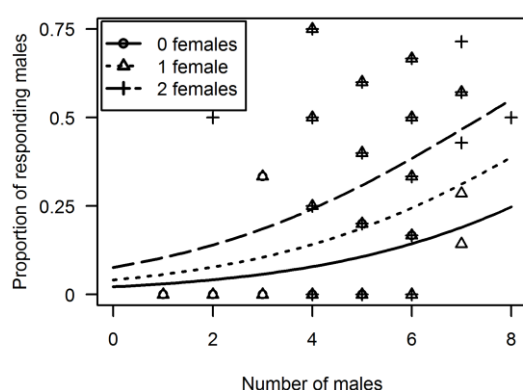


Figure 4: Probability of the proportion of males that responded to long calls in the area as a function of the number of males present and the number of sexually attractive females. The prediction line refers to the binomial GLM predictions

Table 5: The effect of food availability, rainfall, the number of sexually attractive females, and the number of males in the area on the proportion of responding males of 109 days spread over a 10-month period. Parameter estimates, associated standard errors and statistical significance as obtained from a binomial GLM

Fixed effects	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-3.745	0.561	-6.673	0.000
Ecological factors				
Food availability	0.010	0.057	0.178	0.859
Rain	-0.015	0.010	-1.467	0.142
Social factors				
nr. of attractive females	0.657	0.230	2.856	0.004
nr. of flanged males	0.336	0.114	2.946	0.003

$\chi^2_{\text{LRT}} = 48.546, p < 0.001$

Discussion

The aim of this study was to characterize the nature of male-male competition in the roving male promiscuity mating system of Bornean orangutans through an examination of their long-distance communication system. Given that with conventional field methods (such as focal animal sampling) it is not feasible to obtain a comprehensive record of all long-distance vocalizations within a sufficiently large area, we instead relied on an automated grid of recorders in the study area. We used data from this acoustic localization system (ALS) to investigate which social or ecological factors underlie male ranging and long-calling decisions. We were able to show that: (i) male presence in the area is a function of local fruit availability; (ii) call rates reflect the number of sexually attractive females and the number of males present in an area; and (iii) the proportion of long call responses and the proportion of responding males show a positive relationship with the number of sexually attractive females as well as with the number of males present in the area.

As expected for a species with a roving male mating system, the number of males present within our study area varied considerably (range: 0 - 8 males, with a mean of 4.211 males) over the 10 months period. We found that fruit availability was the only significant predictor (Table 2). Interestingly, local fruit availability did not affect the long-calling behavior of males once present (Table 3, 4, 5), suggesting that flanged males are looking for areas with high fruit availability, and subsequently vocally react to the presence of fertile females and other males.

Because male distribution is widely believed to be primarily driven by mating opportunities (Emlen and Oring 1977; Kappeler and van Schaik 2002), the obvious expectation is that males rove in search of females and decide based on cues of the presence of receptive females (Dunbar 2000). The empirical data on Bornean orangutan males, perhaps revealed that the availability of receptive females had no direct effect on male presence. Since female orangutans do not advertise their reproductive status, this may be the best males can do. Moreover, since female orangutans are generally ready to conceive when they exceed a certain condition threshold after a long and energetically draining period of lactation (van Schaik and van Noordwijk 1985; Knott 2001, 2005), which is likely to happen when local food abundance is propitious (MAvN, unpublished data). Thus, local fruit availability is perhaps the most reliable environmental proxy available to males to gather information on the distribution of mating opportunities. Fruit abundance may actually vary considerably over short distances, even in a swamp forest (Harrison et al. 2016), and it therefore pays for males to base their ranging decisions on this ecological variable. Doing so, moreover, helps males to maintain a good physical condition, which seems crucial in the energetically demanding acts of mate guarding and engaging in aggressive male-male conflict (see below).

Although fruit abundance affected a male's local presence, it did not affect his calling behavior, which was exclusively driven by social variables. Average long-calling rates were best predicted by the number of sexually attractive females and the number of other males in the area (Fig. 2, Table 3). This relationship may simply reflect attempts to attract females, and therefore scramble competition. However, closer examination of the nature of long call interactions between males suggests otherwise. Both the proportion of long call responses and the proportion of males that responded to the long calls of other males increased with both the number of sexually attractive females and the number of males in the area (Fig. 3, 4, Table 4, 5). Competition thus becomes more intense when more receptive females are around but also with more rival males present, a pattern in line with predictions from unstable contest competition (Table 1). Comparable results were also found in humans and gorillas but they do not engage in confrontational assessment (Flinn 1988; Sicotte 1994).

It remains somewhat puzzling exactly how males locate sexually attractive females. We can envisage three different mechanisms. First, as mentioned above, males' ranging decisions seem to depend on fruit availability. The likelihood to meet receptive

females in areas with better food supply might be higher and therefore males in such areas are willing to confront others. However, since receptive females are rare as a result of 7-year birth intervals and virtually no infant mortality (Wich et al. 2004, for Tuanan: MAVN, unpublished data), this does not appear to be plausible. Second, females should maximize the probability to mate with the best male, especially when there is no male investment in rearing offspring, or to mate with different males in order to confuse paternity and reduce the risk of infanticide, especially when dominance ranks among males are unstable (Andersson and Iwasa 1996; van Schaik 2000; Andersson and Simmons 2006). Either way, females gain from provoking interactions between a mate-guarding (consorting) male and another calling male by simply approaching the calling male (Cox and Le Boeuf 1977; Fox 2002). The guarding male either drops off or meets the challenge, allowing the female to either select the strongest male as mate or confuse paternity by mating with multiple males. In this case, then, the females are responsible for the escalation among the calling males—a suggestion supported by observations on both Sumatran and Bornean orangutans (Utami and Setia 1995; Fox 2002; Tuanan: BS, unpublished data). Third, because males increase their call rate when informed about the presence of receptive females and increase their competitive call interactions toward rivals, information about the presence of fertile females will automatically spread. Thus, non-intended listeners will be informed immediately. It has been shown that context is encoded in orangutan long calls. This makes it possible for eavesdroppers to extract information by listening to long calls and long call interactions (Spillmann et al. 2010). It is therefore likely that males use a combination of overall calling rate, response rates, and the acoustic properties of long calls to assess the presence of receptive females in the area, even before they have directly observed their presence.

If long call production per se were energetically costly, we should have found a relationship between fruit availability and a male's long call activity. Since this was not the case, we can assume that long call production, at the observed rate of 3.31 (SD = +/- 1.41) per day, is not costly in the energetic sense but rather costly in the social sense because calling males and especially responding males accept the risk of physical fights. Rain as a more direct ecological factor did not influence call activity in the area. Wiley and Richards (1982) argued that long distance communication is strongly affected by noise (i.e. rainfall) that influences detection and discrimination by the receiver. The absence of a relationship between rainfall and long call activity and long call responses in our ALS

models, suggests that rain affects the actual timing of long calls, but not the calling rates over the whole day.

Overall, then, males zoom in on particular areas based on local food abundance and adjust their long-calling behavior to the presence of both other males and sexually attractive females. The responses to other males in the absence of sexually attractive females allow the males to update their information on each other's relative fighting ability, which presumably undergoes appreciable fluctuations (see below). Our observations are not consistent with scramble competition, but rather with the unstable form of contest competition (terminology following van Schaik and van Noordwijk 1988) we call *confrontational assessment*: increased advertising and assessment of rivals' fighting ability when there are sexually attractive females present. This is consistent with the known differences between the social systems of the two orangutan species. In Sumatran orangutans, long call activity is affected by neither social nor ecological factors, indicating that call activity is relatively stable in an area. This is because the dominant male creates an acoustic safety zone that subordinate flanged males avoid and females tend to stay in earshot association with the dominant male in the area (Singleton and van Schaik 2002; Delgado 2003; Mitra Setia and van Schaik 2007). In contrast, in Bornean orangutans the dominance hierarchy among flanged males is much less stable and females with dependent offspring do not seek to remain in earshot association with them (Mitani 1985a; Spillmann et al. 2010), probably because doing so would not guarantee reduced harassment (Bornean flanged males are known to force matings: MacKinnon 1974; Galdikas 1981; Schurmann 1982; Mitani 1985a; Knott 2009) given the rapid fluctuations in conditions and thus dyadic dominance status.

Indications for a less stable dominance system in Bornean flanged males are higher rates of chases between rivals and more observed physical fights among Bornean flanged males compared to Sumatran flanged males. This is also reflected in a significantly higher incidence of scars and mutilated or missing fingers and toes in Bornean males (L. Dunkel, unpublished data). In addition, the proportion of flanged males to unflanged males is much higher in Borneo than in Sumatra, consistent with the lack of developmental arrest of unflanged males in Bornean compared with Sumatran orangutans (Utami et al. 2002; Pradhan et al. 2012; Dunkel et al. 2013; Marty et al. 2015). Moreover, a larger number of flanged males converging around a single female will act to reduce the monopolization

ability of the top-dominant male, and thus create mating opportunities for non-dominant males (Watts 1998).

These results, based on the long-distance communication system alone, suggest that a certain fairly small proportion of flanged males do commit to contest. Another proportion emit long calls but only when circumstances permit it, so as to avoid escalated male aggression that might lead to energetic costly chasings or even more costly physical fights. Field data (B. Spillmann, unpublished data) show quite a bit of turnover between the competitive and non-competitive strategy. Flanged males might extensively compete until they fall below a minimal condition threshold, upon which they cease call interactions to recover from their poor physical condition. This temporally exaggerated competitive behavior resembles the system observed among male elephants: bulls in musth compete intensely over access to females and their condition declines over the course of their musth period (Poole 1987; Poole et al. 2011). Other males avoid contests with musth males, even if these are smaller.

In conclusion, this study shows a combination of scramble and contest components in male-male competition in a roving male mating system among Bornean flanged males. This mix seems to be based on confrontational assessment, where flanged males increase their call rate to attract females and continuously update their dominance relations through commitment in long call interactions, which may result in close encounters and even fights. We suggest that the use of ALS can also enhance our knowledge of male strategies in other species with roving males that call.

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Chapter 3

Who shall I say is calling? Validation of a caller recognition procedure in Bornean flanged male orangutans (*Pongo pygmaeus wurmbii*) long calls

Brigitte Spillmann¹, Carel P. van Schaik¹, Tatang M. Setia², Seyed Omid Sadjadi³

¹Anthropological Institute and Museum, University of Zurich, Zurich, Switzerland

²Fakultas Biologi, Universitas Nasional, Jakarta, Indonesia

³IBM Research, Yorktown Heights, NY, USA

Abstract

Acoustic individual discrimination has been demonstrated for a wide range of animal taxa. However, there has been far less scientific effort to demonstrate the effectiveness of automatic individual identification, which could greatly facilitate research, especially when data is collected via an acoustic localization system (ALS). In this study, we examine the accuracy of acoustic caller recognition in long calls (LCs) emitted by Bornean male orangutans (*Pongo pygmaeus wurmbii*) derived from two datasets: the first consists of high-quality recordings taken during individual focal follows (N = 224 LCs by 14 males) and the second consists of LC recordings with variable microphone-caller distances stemming from ALS (N = 123 LCs by 10 males). The LC is a long-distance vocalization. We therefore expect that even the low-quality test-set should yield caller recognition results significantly better than by chance. Automatic individual identification was accomplished using software originally developed for human speaker recognition (i.e., the MSR identity toolbox). We obtained a 93.3 % correct identification rate with high quality recordings, and 72.23 % with recordings stemming from the ALS with variable microphone-caller distances (20-420 m). These results show that automatic individual identification is possible even though the accuracy declines compared with the results of high quality recordings due to severe signal degradations (e.g., sound attenuation, environmental noise contamination, and echo interference) with increasing distance. We therefore suggest that acoustic individual identification with speaker recognition software can be a valuable tool to apply to data obtained through an ALS, thereby facilitating field research on vocal communication.

Introduction

Acoustic individual recognition can be a very useful tool in studies using passive acoustic monitoring (PAM) for applications such as censuses or acoustic localization systems (ALS) for tracking individuals. The presence of individually distinctive acoustic characteristics in calls or songs has been demonstrated for a wide range of animal taxa, from anurans (Bee et al., 2001) and birds (Ehnes and Foote, 2015) to mammals (Townsend et al., 2014), including non-human primates (Wich et al., 2003). These differences are used for individual recognition in a wide range of animal taxa and modalities, as indicated by playback experiments (Cheney and Seyfarth, 1982, Rendall et al., 1996), stressing the role of individual recognition in molding social behavior (Tibbetts and Dale, 2007). It might therefore be beneficial for studies using PAM to extract caller identities in order to address biologically meaningful research questions about the social behavior of the study species, such as territoriality, aggressive competition, mate attraction, etc. Nevertheless, although most of the studies addressing vocal individuality show that it is possible to discriminate among individuals, it has turned out to be quite challenging to achieve reliable identification of individuals.

Two classes of feature extraction approaches are in use for individual recognition: statistical and non-statistical (Cheng et al., 2010). The former, commonly used for animal calls, relies on measurements of the acoustic call structure from waveform or spectrographic representations of recorded calls (Galeotti and Sacchi, 2001, Peake and McGregor, 2001, Gilbert et al., 2002, Kirschel et al., 2009, Xia et al., 2012). The latter class, which is commonly adopted in human speaker recognition systems, includes linear prediction-based cepstral coefficients (LPCCs) and mel-frequency cepstral coefficients (MFCCs). In the MFCC feature extraction procedure (see Figure 1), on which we focus here, acoustic waveforms are transformed into compact feature vectors on a frame-by-frame basis taking into account an approximate model of human's auditory perception. This auditory perception model is reflected in the mel-frequency scale (Davis and Mermelstein, 1980). An example of the auditory-inspired mel-scale filterbank with 27 channels is provided in Figure 2. This cepstral representation captures the vocal tract resonances, and is based on the source-filter model of human speech production, which is also used to describe the vocal production system in many animal species (Fitch, 2006, Taylor and Reby, 2010). Compared with MFCC extraction, manual acoustic feature

extraction is time consuming and influenced by the researcher’s intuition-based decisions on which parameters to extract. In contrast, MFCC extraction is fully automated, repeatable, and standardized (Mielke and Zuberbühler, 2013).



Figure 1: Schematic block diagram of the MFCC front-end component of speaker-recognition systems.

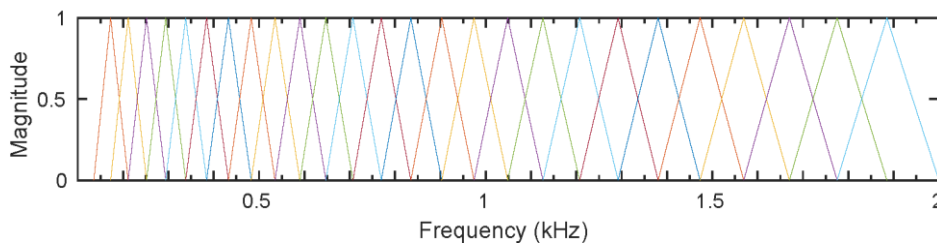


Figure 2: Example of a 27-channel mel-filterbank spanning the frequency range [100-2000] Hz.

Belin (2006) argues that many of the “voice perception” abilities might be shared between human and non-human primates. Therefore, MFCC feature representations might be good candidates for caller recognition studies in non-human primates. Other reasons to use MFCCs in our Gaussian mixture model (GMM) based framework exist as well. First, thanks to the discrete cosine transform (DCT) used in their calculation, MFCCs tend to be uncorrelated and can thus be more efficiently modeled using GMMs with diagonal covariance matrices, as applied to text-independent individual recognition, which works regardless of the actual words being spoken. Second, noise robustness of the MFCC features has been demonstrated in several previous studies (Quatieri, 2002, Clemins et al., 2005, Fox et al., 2008). Third, MFCCs show high accuracy, stability, and repeatability (Cheng et al., 2010). And finally, MFCCs are now also increasingly applied to caller recognition of animals such as elephants (Clemins et al., 2005), passerine birds (Trawicki et al., 2005, Fox, 2008, Cheng et al., 2010), toothed whales (Brown et al., 2010), and blue monkeys (Mielke and Zuberbühler, 2013).

As shown in Figure 3, speaker recognition systems consist of two stages, namely feature extraction (i.e. MFCCs as mentioned above), also called front-end, and

classification, also called back-end, where acoustic space (i.e., distribution of acoustic features) for each speaker is estimated using GMMs (enrollment) and subsequent verification trials are used as validation (Sadjadi et al., 2013). Sadjadi et al. adopted a GMM-UBM framework, where the universal background model (UBM) is a GMM that is trained on a pool of data from a number of speakers (or here: callers). Ideally, the UBM should reflect actual operating acoustic conditions at hand (i.e. background noise). There are also speaker-specific (or caller-specific) models that are adapted from the UBM using the maximum a posteriori (MAP) estimation approach. After the enrollment phase, each test call is scored either against all enrolled speaker models to detect who is calling (speaker identification), or against the background model and a given speaker model to accept/reject an identity claim (speaker verification) (Reynolds et al., 2000). Here, two scenarios are possible: in the first case, this identity claim refers to a closed-set where the speaker or caller is known a priori to belong to a set of M speakers (callers). In the second case, a speaker or caller does not belong to the set, which is called an open-set scenario. In the latter case a threshold value is needed to decide whether a speaker (caller) belongs to the set or is out of the set (Ramachandran et al., 2002).

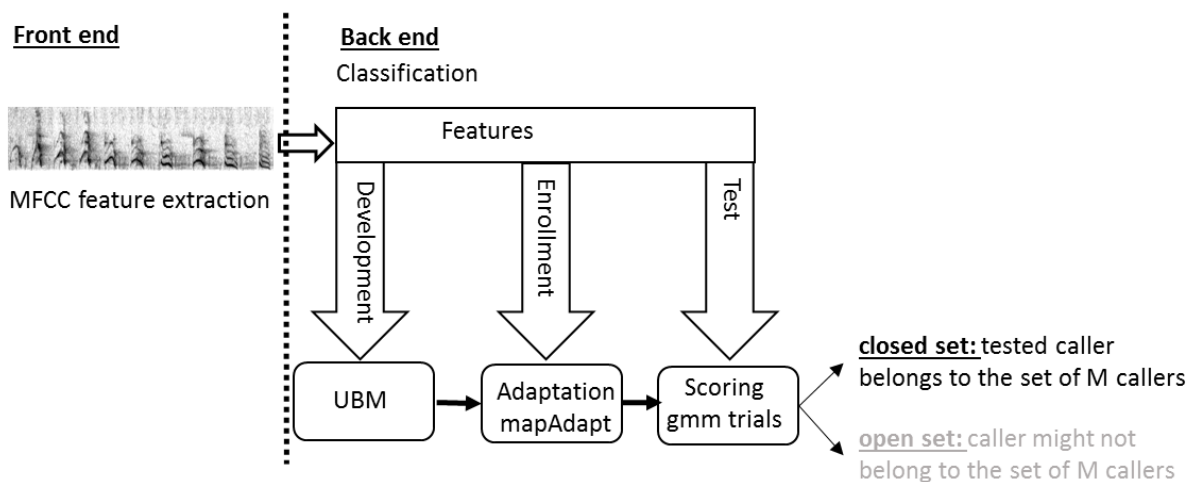


Figure 3: Two stages of speaker recognition system: MFCC extraction in the front end and classification procedure in the back end.

Almost all the previous studies on individual identification used MFCCs that were extracted from high-quality recordings with close-range microphone-caller distances. But

in the case of an ALS with stationary microphones, microphone-caller distances, and thus the quality of the signals, are highly variable. In this study we test the accuracy of an automatic caller recognition approach in orangutan (*Pongo pygmaeus wurmbii*) long calls (Figure 4). The long call is a series of pulses of different pulse types and of highly variable total duration, and discrimination has been reported on a geographic, individual, and contextual level (Delgado, 2007, Ross and Geissmann, 2007, Spillmann et al., 2010). We test two sets of long call recordings in order to match recording conditions (Ramachandran et al., 2002): (i) recordings recorded with short microphone-caller distance (10-20 m) using a Sennheiser ME67 directional microphone during individual focal follows to evaluate the feasibility of this approach in general, subsequently referred to as high-quality recordings, and (ii) recordings from a microphone grid (ALS), with lower signal-to-noise ratios (SNR) due to increased and variable microphone-caller distances and the omnidirectional characteristics of the SMX-II microphone, subsequently referred to as low-quality recordings. We test the validity of this procedure in such a system (more details on ALS see Spillmann et al. 2015) .

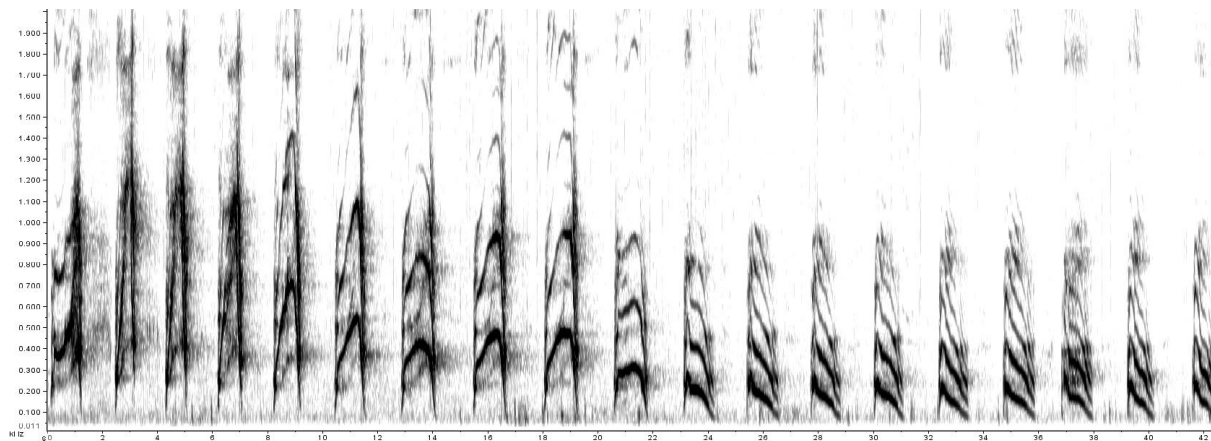


Figure 4: Spectrogram of a long call as used for MFCC extraction

A speaker recognition system can be text-dependent or text-independent. The difference between the two is that in the text-dependent system a fixed phrase needs to be spoken by each individual whereas in the text-independent system no restriction exists in this respect (Ramachandran et al., 2002). The GMM-UBM framework we employed is text-independent. We used this text-independent approach for two reasons: (i) the long calls produced by flanged male orangutans consists of various distinct pulse types (Ross

and Geissmann, 2007, Spillmann et al., 2010), and (ii) long call duration is highly variable ranging from 18 seconds up to 3 minutes (Delgado, 2007). Previous work used acoustic measurements taken at particular pulse types (Delgado, 2007, Spillmann et al., 2010) to demonstrate the feasibility of individual discrimination (not to be mistaken with automatic identification).

We approach the challenge of individual identification of long-calling orangutan males with a software originally developed for human speaker recognition. We used MFCCs for feature extraction available in Matlab Voicebox (<http://www.ee.ic.ac.uk/hp/staff/dmb/voicebox/voicebox.html>) as front-end, and the GMM-UBM framework available in the MSR identity toolbox in Matlab (Sadjadi et al., 2013) as back-end for speaker recognition in order to validate the potential of caller recognition in orangutans applied to a closed set of individuals.

Methods

Study area

Long call recording data presented here stem from Tuanan field station in Central Kalimantan, Indonesia (2.151° South; 114.374° East). The field site is part of an area managed by a non-governmental organization (Mawas) and covers a 1,000 ha trail-system in a peat swamp forest that previously underwent selective logging 20 years earlier. Researchers and well-trained, long-term field assistants conducted individual focal follows according to the standardized field methods (available online at <http://www.aim.uzh.ch/Research/orangutannetwork/FieldGuidelines.html>). This research project adhered to the American Society of Primatologists (ASP) principles for the ethical treatment of non-human primates.

Caller recognition

High-quality recordings

During individual focal follows of flanged male orangutans long calls were recorded whenever possible. We used a Sennheiser ME67 shotgun microphone in combination with a Roland Edirol R09 digital recorder. Recordings were taken at distances of around 10 –

20 m from the calling male with a sample rate of 44.1 kHz and sample size 16-bit. We tested 224 long calls given by 14 different individuals. Recordings were taken during 2007 – 2013. We tested the accuracy of caller recognition by using the Matlab MSR Identity toolbox (Sadjadi et al., 2013). Because the frequency content of the recordings is limited to at most 3 kHz, the original recordings were re-sampled to 16 kHz to increase the computational efficiency of the subsequent processing for the caller identification task.

Three main steps are involved in the speaker recognition procedure: (1) extraction of MFCCs from all waveforms, (2) training of the recognition algorithm with Gaussian mixture models (GMM-UBM framework), and (3) scoring each test call against all speaker models established in the training phase to determine the caller's identity. We divided the long call data into 4 different training sets (80% of an individual's calls) and 4 different test sets (20% of an individual's calls). Each established verification is scored and assigned to a probability value of matching the identified individual through the GMM-UBM framework.

We ran two different caller recognition tests with the sampled high-quality recordings. The first one included MFCC extractions established with mel frequency filters adjusted to the range 100-2000 Hz. The second test included MFCC extractions with mel frequency filters adjusted to the range 130 – 1400 Hz, reflecting the available frequency range of far-distance recordings where sound degradation acted on higher frequencies (see below ALS recordings). We aimed to test whether lower frequency ranges downgrade accuracy of caller recognition and if so to what extent.

To test whether the probability of identification of the GMM-UBM framework predicted identification, we ran a binomial generalized linear mixed model (GLMM) with correctness of recognition as response variable and the GMM-UBM probability of recognition as predictor, including individuals as random effect.

Recordings from the ALS

The microphone grid consisted of 20 omnidirectional SMX-II microphones in combination with SM2 recorders and covered an area of 450 ha localization area at Tuanan field site (Spillmann et al., 2015). Sample rate was set to 22.05 kHz but was subsequently down-sampled to 16 kHz in order to increase the computational efficiency of the speaker

recognition system. We tested long calls recorded by the ALS with known identity due to individual focal follow data where time and location of calling is recorded. We were able to establish an ALS data set with long calls given by 10 individuals, with a total number of 123 long calls to test caller recognition with known microphone-caller distances. We selected long call recordings that showed the whole frequency range of the fundamental frequency in the spectrographic representations and without interfering background noise by conspecific (long call overlap) or heterospecific sounds (e.g. gibbon songs, pigtail macaque calls) but also noise of anthropogenic origin, such as the sound of boat engines. Microphone-caller distances varied between 20 – 420 m. As with the recordings made during focal follows, mel frequency filters were adjusted to the range 130-1400 Hz. Similar to our previous experiment, we divided the long call data into 4 different training sets (80% of an individual's calls) and 4 test sets (20% of an individual's calls). In order to visualize the performance of the caller recognition procedure we established a confusion matrix which contains information about the actual and predicted classification done by the GMM-UBM framework.

As with the focal-animal recordings, we also used a binomial GLMM to test whether the probability of identification of the GMM-UBM framework, the microphone-caller distance and the angle between call direction and microphone position (see Figure 5) were valuable predictors for correct or incorrect identification. We used 4 categories for the angle-variable: 1 = long call direction $<45^\circ$; 2 = LC direction $>45^\circ <90^\circ$; 3=LC direction $>90^\circ <135^\circ$; and 4= LC direction $>135^\circ <180^\circ$. We controlled for the possible impact of individuals by entering them as random effect.

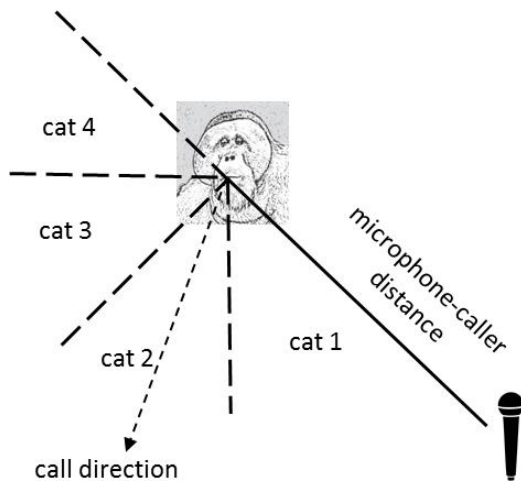


Figure 5: microphone-caller distance and angle between call direction and microphone. We used 4 angle categories. The example in the figure shows a call direction of angle category 2 ($>45^\circ <90^\circ$) in relation to the microphone position.

Results

High quality recordings

We used automatic speaker recognition software to establish the accuracy of orangutan long call identification of high quality recordings with microphone-caller distances between 10-20 m. We ran the identification procedure two times with different filterbank configurations for MFCCs. The frequency range 100-2000 Hz resembles the frequency distribution of a long call and with this range we obtained a 93.32 % correct caller recognition rate. In order to test the accuracy of the smaller bandwidth that resembles the bandwidth of lower quality recordings, we extracted MFCCs between 130 – 1400 Hz of the same dataset as above and observed a slight degradation in accuracy with a 90.66 % correct caller recognition rate (Table 1). Thus, there was a marginal reduction in accuracy of around 3 % with the reduced bandwidth.

Table 1: Results of caller recognition using high quality recordings from 14 individuals with 224 identifications.

Frequency range (Hz)	1. set	2. set	3. set	4. set	average	range
	% of correct assignments					
a 100-2000	91.07	91.07	94.64	96.49	93.32	91.07 - 96.64
b 130-1400	87.5	85.71	96.43	92.98	90.66	85.71 - 96.43

We examined with a binomial GLMM whether the probability value of the GMM-UBM framework is a valuable predictor for correctness of caller recognition. We corrected for individual impact by entering them as a random effect. Both statistical models with datasets a (full bandwidth) and b (reduced bandwidth) showed that the probability value of the GMM-UBM framework is a highly significant predictor for correctness of caller identification (see Table 2a & 2b).

Table 2a and b: The effect of the probability value (a) full bandwidth of long calls and (b) reduced bandwidth on correctness of caller identification. Parameter estimates, associated standard errors and statistical significance as obtained from a binomial GLMM

Dataset a	Estimate	Std.Error	z value	Pr(> z)
(Intercept)	-17.145	3.863	-4.438	
probability	33.68	7.026	4.794	<0.001
$\chi^2_{\text{LRT}} = 47.005, p < 0.001$				

Dataset b	Estimate	Std.Error	z value	Pr(> z)
(Intercept)	-9.044	3	-3.015	
probability	19.491	5.24	3.72	<0.001
$\chi^2_{\text{LRT}} = 19.838, p < 0.001$				

Recordings from the ALS

In a next step, we tested the accuracy of long call identification with variable microphone-caller distances (20 – 420 m). We ran the identification algorithm for 123 long calls given by 10 individuals, and found that 72.23 % of calls were correctly identified (Table 3). The confusion matrix (see Table 4) of caller recognition shows the results for each tested individual for distances < 420 m and distances < 300 m, with the improvement of identification with shorter microphone caller distances indicated in bold. The result of the binomial GLMM shows that the probability value of the GMM-UBM framework best predicts correct or incorrect assignments (see Table 5) but also that increasing microphone-caller distance negatively affects identification (Figure 6) whereas an increasing angle between call direction and microphone shows a tendency to do so too (see Table 5).

Table 3: Results of caller recognition using long call recordings from the microphone grid with variable caller-microphone distances (20-420 m). Sample consisted of 123 long calls given by 10 individuals

frequency range (Hz)	1. set % of correct assignments	2. set	3. set	4. set	average	range
130-1400	77.41	80.64	63.33	67.74	72.28	63.33 – 80.64

Table 4: Confusion matrix of caller recognition with variable microphone-caller distances. Improvement of caller recognition by reducing microphone-caller distance from < 420 m to < 300 m denote in bold.

		Classification										% correct
		Chili	Dayak	Helium	Henk	Katman	Otto	Preman	Teju	Tomi	Wodan	
Label	Chili	12/11	0	0	1/1	0	5/4	1/1	1	0	0	60.00/ 61.11
	Dayak	1	4/2	0	0	0	0	0	0	0	0	80.00/66.67
	Helium	1	0	13/12	0	0	3/2	0	0	0	0	76.47/ 80.00
	Henk	1	0	1/0	3	0	1/0	0	1/0	0	0	42.86/ 75.00
	Katman	0	0	0	0	7	1	0	0	1	0	77.78
	Otto	1	0	0	0	0	8/7	0	0	1	0	80.00/77.78
	Preman	0	0	0	0	0	2/1	5	1	0	1/0	55.56/ 80.95
	Teju	1	0	0	0	0	2	1	17	0	0	80.95
	Tomi	0	0	0	0	1	0	0	0	8	2/1	72.73/ 80.00
	Wodan	0	0	0	0	0	0	1	1	0	12	85.71

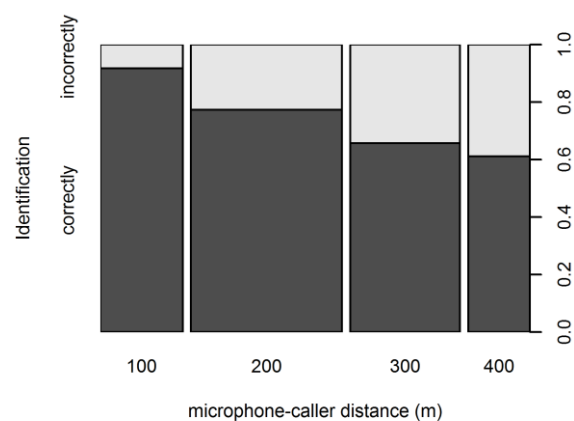


Figure 6: Likelihood of correct identification with increasing microphone – caller distances.

Table 5: The effect of the probability value, the microphone-caller distance, and the angle calling direction-microphone on correctness of caller identification. Parameter estimates, associated standard errors and statistical significance as obtained from a binomial GLMM

fixed effects:	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-24.317	7.077	-3.436	
probability	46.317	13.126	3.529	<0.001
microphone-caller distance	-0.760	0.321	-2.369	0.018
angle calling direction-microphone	-1.279	0.674	-1.897	0.058

$\chi^2_{LRT} = 32.63, p < 0.001$

Discussion

The aim of this study was to test the potential of an automatic speaker recognition system (originally developed for human voice recognition) applied to orangutan long calls. High-quality recordings with close-range microphone-caller distance (directional microphone) yielded 93.3 % (by chance 7.14 %) correct caller recognition (Table 1). Low-quality recordings (omnidirectional microphone) and variable, usually far greater, microphone-caller distances (20-420 m) yielded 72.28 % (by chance 10 %) correct caller recognition (Table 3). These results reflect the ability of individual recognition known from experimental tests in different primate species (i.e. Snowden and Cleveland, 1980, Cheney and Seyfarth, 1982, Rendall et al., 1996). In both cases (high- and low-quality recordings), the probability value of the GMM-UBM framework can be used as a benchmark for correctness of caller recognition. This result indicates that high probability values indicate more confidence in accuracy of the identification result (Table 2 & Table 5). As expected, microphone-caller distance had a negative effect on the accuracy of caller recognition, whereas the angle between call direction and microphone tended to do this too (Table 5 & Figure 6).

The degradation of accuracy in caller recognition from high-quality recordings to low-quality recordings was expected, but despite the large variation of microphone-caller distances the result of the low quality recordings (72.28 %) is still far above the identification success expected by chance of 10 % (for 10 individuals). The different microphone-caller distances incorporate much variation based on biotic and abiotic factors. Biotic factors include background noise caused by other animal calls or by anthropogenic origin (noise of boat engines), and degradation of sounds by the vegetative structure of the location. Abiotic factors include attenuation of sounds due to the distance

of the recorded call, or weather- or climate-related effects (Kirschel, Earl et al. 2009). A major limitation in applying the validated method is distance. Our result suggests that long call identification at far distances yields lower accuracy due to sound attenuation and signal degradation that results in low SNR. Nevertheless, our approach yields a remarkably high accuracy in light of the highly variable microphone caller distances. Indeed, another study that tested individual discrimination of long calls by applying acoustic measurements of re-recorded playbacks at different distances, found possible discrimination up to 300 m (Lameira and Wich, 2008). Additionally we found a tendency of a negative effect of the angle between call direction and microphone, which implies that long calls may have a directional characteristic.

Our results suggest that automatic individual identification is reliable for distances up to 420 m. The limitations of this approach are sound degradation and background noise that masks the signal of interest. This raises the question whether these processes also impair the orangutans' ability to recognize the identity of the long-caller at farther distances. Evidence for improved perception of a target signal in spite of noise and degradation comes from the so called cocktail party effect encountered in human and animal communication literature, where selective attention tunes out all but the signal of interest (Aubin and Jouventin, 1998, Ebata, 2003). Obviously, group living animals may face the cocktailparty problem, but also heterospecific signalers may contribute to a receiver's perception problem (Bee and Micheyl, 2008). In orangutans the latter incidence is plausible: orangutans are semi-solitary and long call overlap is rare, but rainforests are quite noisy habitats (Slabbekoorn, 2004). In future work, we plan to test whether responses to distant long calls deviate from those to closer ones.

In conclusion, this study demonstrates that an automatic speaker recognition system originally developed for human voice recognition provides a promising and viable tool for animal vocal communication research and in particular for the identification of calling individuals recorded by a passive acoustic monitoring system. Note, however, that the validation presented here considered a closed-set scenario, and that when applying this method to passive acoustic monitoring data without knowledge of the caller identity, an open-set approach is required to account for new individuals that may move into a monitored area. We propose that automatic caller recognition is a valuable tool to identify individuals by their calls stemming from passive acoustic monitoring and acoustic localization systems. Its use can greatly facilitate field research on vocal communication.

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Chapter 4

Long calls as indicators of contest motivation

Brigitte Spillmann¹, Erik P. Willems¹, Maria A. van Noordwijk¹, Tatang Mitra Setia², Carel P. van Schaik¹

¹Anthropological Institute and Museum, University of Zurich, Zurich, Switzerland

²Fakultas Biologi, Universitas Nasional, Jakarta, Indonesia

Abstract

Dominance in social animals is usually dyadic, and measures used to estimate it reflect this. In some species, however, the social context is rather unstable. This means that an individual's estimate of a rival's fighting ability may be absent or out of date, and the best he can do is to assess one's own fighting ability relative to the majority of others likely to be encountered, while relying on dyadic dominance relations for those met regularly. Here, we study wild male Bornean orangutans. Flanged males are solitary, roaming around in search of fertilizable females and emitting long calls that repel rivals. We used an acoustic localization system, a grid consisting of 20 recorders that recorded long call events over a period of 10 months, combined with individual focal follow data collected over an 8-year-period to estimate individual males' call and response rates to examine whether long calling behavior reveals fluctuation in fighting motivation. We show that males decide to confront or withdraw based on their fighting motivation by comparing their call and response rates with those of their rivals, whereas high-intensity agonistic encounters happen when males encounter rarely met or new rivals with whom they lack a decided dominance relationship. Therefore, the Bornean orangutan males' long calls are mediators of contest motivation.

Introduction

Whenever it is possible for individuals to exclude others from access to critical resources (contest competition), rather than being forced to share it with others (scramble), we expect overt conflicts over access (Enquist and Leimar, 1987, Janson and van Schaik, 1988, Dunbar, 2000). Repeated encounters between the same competing individuals will lead to dominance relationships, where the outcome of such an interaction can be predicted (Dunbar, 1988), and escalated fights are avoided through signaling and asymmetric avoidance (de Waal, 1986). The establishment of such dyadic dominance relationships assumes that individuals know each other, remember the outcomes of previous encounters, and have accurate and updated information about each other's relative fighting ability and motivation (Preuschoft and van Schaik, 2000). In stable social groups, therefore, we usually see linear dominance hierarchies, where individual dominance ranks are tightly correlated with their current fighting ability, and where changes in dominance rank are linked to changes in relative fighting ability (Preuschoft and van Schaik, 2000).

In systems where individuals often meet strangers or known individuals they have not met for some time and fighting ability may change rapidly over time, they must assess their own relative fighting ability whenever they meet. The outcome of agonistic encounters can often be predicted by asymmetries in the size, weight, physical condition or weaponry of the individuals (Clutton-Brock and Albon, 1979a, Pelletier and Festa-Bianchet, 2006), although this becomes harder as differences in the prior attributes become smaller (Hughes, 1996). Lengthy assessment, and especially damaging escalated contests, can be avoided where honest signals of fighting ability are displayed during the assessment (Huntingford and Turner, 1987). Secondary sexual characteristics often convey information about relative fighting ability, as shown in roe deer's antler size (Vanpé et al., 2007), canine tooth size in mandrills (Leigh et al., 2008), or status badges in various birds (Rohwer, 1982, Møller, 1988, Lantz and Karubian, 2016). All such signals allow rapid assessment of one's own fighting ability relative to that of each opponent, and thus the probability of winning (Parker, 1974).

Acoustic signals are common in male-male competition and female attraction in taxa as diverse as anurans, birds, and ungulates (Clutton-Brock and Albon, 1979a, Searcy and Andersson, 1986, McComb, 1991, Reby et al., 2005, Martínez-Rivera and Gerhardt,

2008), but less pervasive in non-human primates (Wich and Nunn, 2002) probably due to the fact that non-human primates tend to know their rivals well and need less to rely on signals that indicate fighting ability. Nevertheless, a prevalent acoustic signal in non-human primate species is the loud call, often emitted by males (Waser, 1982, Mitani and Stuht, 1998, Wich and Nunn, 2002) and used in intergroup spacing and intragroup cohesion (da Cunha and Byrne, 2006, Salmi and Doran-Sheehy, 2014). Loud calls evolved to serve in resource defense and mate attraction (Wich and Nunn, 2002), and some studies have shown that loud calls are a sexually selected signal in non-human primates that may enable assessment of fighting ability (chacma baboon; Kitchen et al., 2003, Fischer et al., 2004, crested macaques; Neumann et al., 2010).

In this study we focus on male competition among orangutans as mediated by their long calls. Delgado (2006) found that male orangutans' loud calls (the so-called long call) fulfill the prerequisites of being a sexually selected signal (Snowdon, 2004) and serve in both male-male competition and female attraction. However, he found no indication of long calls being costly in terms of production. Compared to ornaments or armaments acoustic signals used in competitive contexts vary over shorter time periods and are therefore more likely to convey information about short-term changes in motivation than in fighting ability (Rubenstein and Hack, 1992, Vehrencamp, 2000). We will test and confirm Delgado's assessment here. This implies that orangutans, although they would greatly benefit from having honest signals of fighting ability, do not have such signals.

An important question therefore is how males regulate their contest competition. Many flanged orangutan males compete for sexual access to a single female because they have very large home ranges relative to females, which also overlap widely (Singleton and van Schaik, 2001, Buckley, 2014). As a result, there is high potential for contest. Some males are frequently sighted, whereas others can be absent for years and show up, and yet other, fully adult or even old males show up for the first time after years of study (B. S., unpubl.). This implies they have variable social knowledge of their rivals fighting ability. Data suggest that Bornean males vary in condition over short periods of time due to the low productivity (Wich et al., 2011, Vogel et al., 2015). Thus, rivals must estimate each other's fighting ability even if they know each other. Especially on Borneo, therefore, males must continuously update their social information and may have to do during encounters.

Assuming stable contest competition, asymmetric avoidance would be expected as suggested for Sumatran orangutans with a locally dominant male in the area that controls the area through his long calls whereby subordinate males avoid him and cease calling (Delgado, 2006, Mitra Setia and van Schaik, 2007). Since it is expected that individual males can recognize each other's long calls (Borneo and Sumatra: Delgado 2006, Spillmann et al. 2010), in a stable system a Sumatran male merely needs to identify his rival (Delgado, 2003). However, a recent study of Bornean orangutans (Spillmann et al., 2017) found that long calls indeed serve in male-male competition (Mitani, 1985), and showed that this competition becomes more intense with the availability of receptive females but also with the number of rivals in an area. This pattern is expected when males often have unstable dominance relations among them, reflected in the difficulty to detect a locally dominant male in Bornean males compared to Sumatran (Galdikas, 1983, Buckley, 2014), the higher incidences of injuries, and the higher ratio of flanged males compared to unflanged males in Bornean males (Dunkel et al., 2013). This frequent confrontation among Bornean flanged males might be a consequence of their social environment that continuously changes over time. A flanged male's presence in Tuanan is a function of local fruit availability, which varies even in swamp forests (Harrison et al., 2016) and may serve to the males as a proxy for the presence of fertile females (Spillmann et al., 2017). In such a system, even though it is known that long calls serve as indicators of individual identity (Delgado, 2003, Lameira and Wich, 2008, Spillmann et al., 2010), mere recognition of callers is not sufficient to assess an individual's relative fighting ability, because on one hand males may have not met for a long time and fighting ability information may be outdated, and on the other hand unknown males moving in an area that are not yet assessed. In testing it, we can ignore the possible effect of relatedness because male orangutans leave their natal area and relatedness analysis of the Tuanan flanged male population revealed that none of them is related (Arora et al., 2012). We will test various predictions that follow from the contest motivation hypothesis by assuming that the long call is a conventional signal that contains no production costs but social costs as the risk of fights and injuries (Vehrencamp, 2000, Delgado, 2006, Laidre and Johnstone, 2013).

1. Testing confrontational assessment on an individual level with indices of long call activity

In a recent study we found that average long-call activity, be it long call rates or response tendency, was a good proxy for the intensity of male calling competition, because it varied with both the presence of a highly valuable resource (receptive females) and the number of competitors (in Tuanan flanged males: (Spillmann et al., 2017)). Because this result was found at the aggregate level (in the absence of caller identification), here we evaluate whether an individual's long call activity is likewise a function of the presence of sexually attractive females.

2. Is long call production energetically costly?

We assume that the calls themselves are not energetically costly in the way handicap signals are, but that being highly vocal bears cost in the social domain which is common in convention and vulnerability signals (Delgado, 2006, Laidre and Johnstone, 2013), so overall rate and especially response patterns may reflect contest motivation since all males would be equally capable to produce calls at similar rates. To exclude the possibility that long calls are “handicap signals” we must test whether long call duration and long call rates are affected by male condition and thus relative dominance status or food abundance. Earlier, we found that fruit availability had no effect on the average male's long call activity, which is an indication that long call production is not energetically costly (Spillmann et al., 2017). Here, we will test this prediction at the individual level by examining the effect of male dominance status (low versus high) on long call duration, both within males over time and across males.

3. Impact of poor social knowledge

The highly variable local presence of males allowed us to divide males into residents and visitors (see methods for criteria used). We therefore predict a relationship between dyad composition (R-R, R-V, and V-V, where R=resident and V= visitor) and the intensity of the agonistic interaction (from chases to fights) as a reflection of the imperfect end of the spectrum of information on rival's fighting ability spectrum.

4. *Does long calling activity indicate contest motivation?*

If social knowledge is limited because of the continuously shifting social environment and the fluctuation of individuals' fighting motivation, we assume more intensive agonistic interactions as the uncertainty of rivals increases. Therefore, we expect that an individual's involvement in agonistic encounters should be a function of an individual's contest motivation, as reflected in his call rate and his tendency to respond to others' long calls.

5. *Is fluctuating fighting motivation reflected in long call activity?*

Theoretical models show that signals can be reliable without inflicting production cost when deviation from the honest equilibrium will be met with high costs apart from production (Owens and Hartley, 1991, Johnstone and Norris, 1993, Laidre and Johnstone, 2013). Therefore, long call activity is not an absolute measurement of fighting ability but rather of fighting motivation, which can fluctuate considerably over time. We predict that a male's fluctuating fighting motivation is reflected in his long call rates; hence, individual call rates should vary both over time and between individuals, but independently of each other. Second, we expect that individual long call response rate is a function of individual long call rate, and that an individual's long call response rate is therefore predicted by his long call rate. Third, we predict that long call responses can be seen as agonistic vocal interactions, and that vocal responses should therefore predict outcomes of chases or escalated fights as a reflection of fighting motivation. We use Elo ratings to capture this fluctuation (see methods for details). Fourth, we predict that, if a male gets seriously injured in a fight (e.g. especially when body parts used in fights are involved), his calling and response rate should decrease to avoid further fights.

We tested these predictions using an Acoustic Localization System (ALS), which included 10 months of automatically recorded long calls from a recorder grid at Tuanan study area, Central Kalimantan, Indonesia. The ALS data gives an accurate picture of male presence and their call activity in the area and is mandatory to address questions about male assessment strategies in a species where individuals are widely dispersed (see table 1 in discussion).

Methods

Study area

Fieldwork was conducted at the Tuanan field station in Central Kalimantan, Indonesia (2.151° South; 114.374° East). The field site is part of the larger Mawas conservation area and covers a 1,000 ha trail-system in a peat swamp forest that had undergone selective logging around 20 years earlier. The local orangutan density, which was ca 4.2 individuals per km² in 2003 (van Schaik et al. 2005), is gradually increasing.

None of the observers were aware of the hypotheses we were testing. This research project adhered to the American Society of Primatologists (ASP) principles for the ethical treatment of non-human primates. It was approved by the Indonesian Ministry for Research and Technology (RISTEK).

Long call data from focal follows

The behavioral data were part of the routine individual focal follow schedule at the field site of researchers and long-term field assistants. Data were collected according to a highly standardized field protocol (see: <http://www.aim.uzh.ch/Research/orangutannetwork/FieldGuidelines.html>). Whenever possible during focal follows of flanged males long calls were recorded with a Sennheiser ME67 microphone and a Roland recording device. We used focal follow data from 2005-2012 to run similar models as collected with the ALS (see supplementary material I, and table 1 in the discussion).

Long call data from the acoustic localization system (ALS)

We installed an acoustic localization system (ALS) consisting of 20 off-line, time-synchronized (via GPS), SM2+ autonomous recording units in a lattice at 500 m intervals, thus encompassing an area of 300 ha. The ALS was programmed to record continuously from 04:30 to 18:30 local time, to cover the orangutan's entire diurnal activity period. In total, we recorded and localized 3118 long call occurrences on 111 days (total 1554 hours x number of recorders), spread out over a period of 10 months (March 2012 – December 2012). In a previous study, we validated the performance of the acoustic detection and

the acoustic localization of long calls. We established that long calls were reliably detected in an area of 900 ha, and also defined a triangulation area of 450 ha, in which acoustic localization was accurate. For more detailed information about signal detection, localization, and assumptions of using the ALS method see Spillmann et al. (2015, 2016). All following analyses consist of individually identified calling individuals (see below).

During the ALS period we also conducted seven playback experiments. These experimental days were excluded from the following analyses. However, days after a playback experiment were included, because when we compared long call occurrences in the area on the day after experiment with the day before experiment, no significant difference was found.

Identification of ALS callers

The dataset consists of 3118 long calls, of which 1923 could be identified with the procedure explained below and were introduced in the following analyses. 1415 long calls were given outside of the triangulation area (see above) where identification was difficult, especially for far out long call. Nevertheless, we were able to identify 81.1% of the long calls given inside the triangulation area and 41.5% of the long calls located outside the triangulation area. Most of the unidentified long calls occurred far outside of the recorder grid. Therefore, we do not assume a bias in this respect.

For the identification, we used a four-step procedure. First, for all males followed as focal animals we knew the time and the location of long calls given, and this information could be matched with long call occurrences in the ALS. Second, we recognized individual callers based on a feature extraction procedure using mel-frequency cepstral coefficients (MFCC) and an identification procedure based on a Gaussian mixture model (GMM)-based framework (see Spillmann et al., 2016, for more details). We used the same training set as used in the study of caller recognition (Spillmann et al., 2016) but added another individual with high idiosyncrasy (noisy voice with low and tight frequency bands). As a result, 11 males qualified for the caller recognition procedure. Caller identifications that reached at least a chance level of >0.8 were considered as possibly correct identifications. Additionally, only sound files were included that were not masked by background noise and for which the fundamental frequency was visible. Noise of boat engines was a limiting

factor to use sound files for caller recognition analysis (Tuanan field site is situated close to the Kapuas river, which is the main transport axis in the area). Third, seven of the males (including the new male included in the caller recognition training) could typically be identified by idiosyncratic structures in the spectrograms of their long calls. Fourth, we applied a time-distance rule that assigned two calls to the same male if they occurred within 4 hours and a 300 m radius from each other under the additional restriction that speed of movement did not exceed 550 m/h. This rule was derived empirically from long call data from focal animal sampling over the course of complete follow days ($N_{\text{total LCs}}=848$ ($N_{\text{focal LCs}} = 242$, $N_{\text{others LCs}} = 606$), 96.8 % correct assignments, false pos. = 10, false neg. = 17).

We combined the different identification steps as follows: We prioritized the identifications made in the focal follow data. Next, we established potential identities according to idiosyncrasies and caller recognition procedures (with chance level > 0.9) (Spillmann et al., 2016). Identifications with chance levels of caller recognition between 0.7-0.9 were only used when they either were confirmed with additional idiosyncrasies in this particular call or with a call given before or after by the same male according to time-distance rule, which was identified via idiosyncrasies or caller recognition (chance level > 0.9). Identifications with chance levels < 0.7 were not integrated in further analyses. Finally, we checked with the time-distance rule (Spillmann et al., 2017) whether the remaining unidentified long calls (usually because signals were masked because of background noise) could be allocated to already identified long calls according to the time-distance rule (supplementary material I: table with percentages of used combination steps for LC identifications).

Resident – Visitor distinction

Males were recognized based on descriptions, photographs and genetic confirmation where needed (after long absences). From the focal follow data we extracted the number of months a male was present (observed) in the area per year. We grouped males into the category visitors when a male was not encountered for > 12 months or met for the first time in the area. A visitor's residence status changed to resident when he was seen for at least 6 months in a year and switched to resident after the fourth month encountered in the study area (for more details see supplementary material II).

Fruit availability

Monthly fruit availability was determined by means of a standardized phenological protocol (<http://www.aim.uzh.ch/Research/orangutannetwork/FieldGuidelines.html>) for ~1500 trees in a 2 ha plot. From these data, a monthly fruit availability index (FAI) is calculated, defined as the *proportion of monitored trees carrying fruit*.

Sexually attractive females

We used the same criteria for the estimation of sexually attractive females as in our recent study (Spillmann et al., 2017). To establish the conception date of a female we used a gestation length of 8.5 months (Graham, 1988). A female was taken to be sexually active up to 6 months before, and 2 months after the time of estimated conception, based on patterns in mating activity (L. Dunkel, unpublished data). Unlike chimpanzees and bonobos, orangutan females do not indicate the peri-ovulatory period through sexual swellings (Galdikas, 1981).

Non-responder versus responder

For any given month, we established whether a male was a responder or non-responder. A responder had responded to at least 1 long call in a given month.

Elo rating

We used Elo-rating (Neumann et al., 2011) to establish Elo scores with immediate long call response data collected with the ALS. This approach is less affected by demographic changes than other methods (e.g. David's score: David, 1987). A responding individual was set as the winner of a long call interaction. Maximal distance of such an event was set to <1300 meters with a latency of < 5 minutes. We calculated from the elo scores the difference of dyad's Elo scores (delta elo) for those dyads that subsequently engaged in an agonistic interaction (chase, fight) observed during focal follows to test the prediction that this difference in current fighting motivation (reflected in Elo scores) can predict the outcome of the upcoming agonistic encounter.

Statistical analysis

First, we fitted a series of models to assess which social (male's residence status, presence of sexually attractive females) or ecological (monthly fruit availability) variables (fixed effects) best predicted aspects of individual long call behavior as a replication of the confrontational assessment on an individual level. All following models included individuals as random effect: (i) for the individual's daily call rate (poisson GLMM); (ii) for the daily response proportion of an individual (binomial GLMM), and (iii) for responder status as a dichotomous variable as being a responder or a non-responder in a given month (binomial GLMM).

Second, we tested whether long call production is energetically costly. We fitted a linear mixed effect model with long call duration as the response variable and individuals' relative dominance status, fruit availability, and context of long calls as fixed effects. We introduced individuals (N = 10) as random effect. The long calls of one particular resident male, Niko, were recorded (N = 48) in different years (2005, 2007, 2011, and 2012). He appeared dominant from 2005-2007 due to regular involvement in agonistic encounters but dropped in this respect later on. We tested with a t-test whether a difference between the two periods of dominance is reflected in the duration of his long calls.

Third, agonistic encounters fall onto the "imperfect" end of the information on rival's fighting ability spectrum: We ran a chi-square test to examine whether there is a relationship between the type of agonistic encounters (chasing versus fights) and the composition of the dyad relating to residence status (resident versus visitor).

Fourth, long calls as a reflection of fighting motivation should correlate with a male's involvement in agonistic encounters. We ran a generalized linear mixed model (GLMM) with binomial distribution. The response variable was being involved in an agonistic encounter in a given month (no-yes). The fixed effect was individual long call rates in one model and being a responder or not in another model. Additionally, individuals were introduced as random effect.

Fifth, we tested whether fluctuation in fighting motivation is reflected in calling behavior. To test whether individual call rate varies among individual and months and across months we fitted a linear mixed effect model with poisson distribution (LC rate/day) as response variable and individuals, time period (months), and the interaction between individual and time period as predictors. We introduced individuals as random

effect. With a generalized linear mixed model (GLMM) we tested whether long call rates (fixed effect) predicts long call response rate per day. We included individuals as random effect. In order to predict the outcome of dyadic agonistic encounters we fitted a generalized linear mixed model (GLMM) with a binomial distribution for the outcome (loser-winner) of an agonistic encounter (iii). We incorporated delta Elo stemming from long call interactions as the main predictor variable. We introduced a random effect with individuals nested in the competing dyad. Long call behavior was tested after winning or losing a fight in which injuries were sustained. We ran several Wilcoxon rank-sum tests of three individuals involved in physical fights (loser and winner). We tested whether their call and response rate changed from the month before the injury to the month after the injury.

For all models the likelihood ratio tests were executed by comparing all variables of each model with the null model. All models were implemented in R3.1.3 (R Core Team, 2015) using the packages lmerTest and MuMin (Kuznetsova et al., 2015, Barton, 2016).

Results

Individual-level confirmation of confrontational assessment using long call activity

We found that an individual male's long call rate per day was a function of the presence of sexually attractive females ($P < 0.001$). Neither a male's residence status (resident versus visitor) nor fruit availability had an effect on his long call rates (see table 1).

Table 1: The effect of males' residence status, sexually attractive females, and food availability on individual long call rates. Parameter estimates, associated standard errors, and statistical significance as obtained from a poisson GLMM

Fixed effects	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	1.033	0.118	8.746	
Males' residence status	-0.087	0.071	-1.240	0.215
Sexually attractive females	0.622	0.089	6.978	<0.001
Food availability	-0.009	0.010	-0.892	0.372
$\chi^2_{LRT(3)} = 65.114, P < 0.001$				

Only 13.1% of all recorded long calls were immediate long call responses (235 responses out of a total of 1923 identified long calls). However, a binomial GLMM ($N = 362$) showed that the response proportion of individual males was best predicted by the

presence of sexually attractive females ($P = 0.021$). Also here, neither residence status of the male nor fruit availability had an effect on the response proportion (see table 2).

Table 2: The effect of males' residence status, sexually attractive females, and food availability on individual long call response proportion. Parameter estimates, associated standard errors, and statistical significance as obtained from a poisson GLMM

Fixed effects	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-2.788	0.380	-7.341	
Males' residence status	0.077	0.224	0.341	0.733
Sexually attractive females	0.819	0.356	2.304	0.021
Food availability	0.012	0.027	0.465	0.642
$\chi^2_{LRT(3)} = 8.156, P=0.042$				

Using a GLMM with a dichotomous response variable as being a non-responder or a responder was largely explained by the presence of sexually attractive females ($P < 0.001$). Resident males tended to be more likely to be a responder than visitor males ($P = 0.061$). Fruit availability had no effect (see table 3).

Table 3: The effect of males' residence status, sexually attractive females, and food availability on being a responder or not. Parameter estimates, associated standard errors, and statistical significance as obtained from a poisson GLMM

Fixed effects	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.1577	1.0841	-0.145	
Males' residence status	1.4038	0.7482	1.876	0.0606
Sexually attractive females	-3.8456	0.8536	-4.505	<0.001
Food availability	0.1072	0.3501	0.306	0.7595
$\chi^2_{LRT(3)} = 63.303, P<0.001$				

Is long call production energetically costly?

We found a significant LMM for long call duration ($N = 264$). If long calls were handicap signals, we should expect an effect of relative dominance status or fruit availability on long call duration, but neither had a significant effect (figures 1 a, b and table 4). The best predictor instead was long call context ($P = 0.001$): elicited long calls on average last longer than spontaneous long calls.

Table 4: The effect of food availability, relative dominance, and context of long call on long call duration. Parameter estimates, associated standard errors, and statistical significance as obtained from a LMM

Fixed effects	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	47.710	5.846	10.900	8.162	
Food availability	0.353	0.609	88.540	0.580	0.564
Rel. Dominance (low-high)	-9.357	6.614	6.600	-1.415	0.203
Context (spontaneous-elicited)	7.591	2.349	191.040	3.231	0.001
$\chi^2_{LRT(3)} = 12.351, P=0.006$					

We also found no effect of relative dominance on long call duration within an individual male (Niko): mean of 46.1 sec (s.d. = 12.79) during his high-dominance period versus 45.8 sec (s.d. = 13.75) during his low-dominance period ($t=-0.071$, $df = 28.224$, $P > 0.05$). These two analyses show that long calls are not energetically costly in the energetic sense, and should therefore be merely costly in the social sense of potentially eliciting responses and thus agonistic encounters.

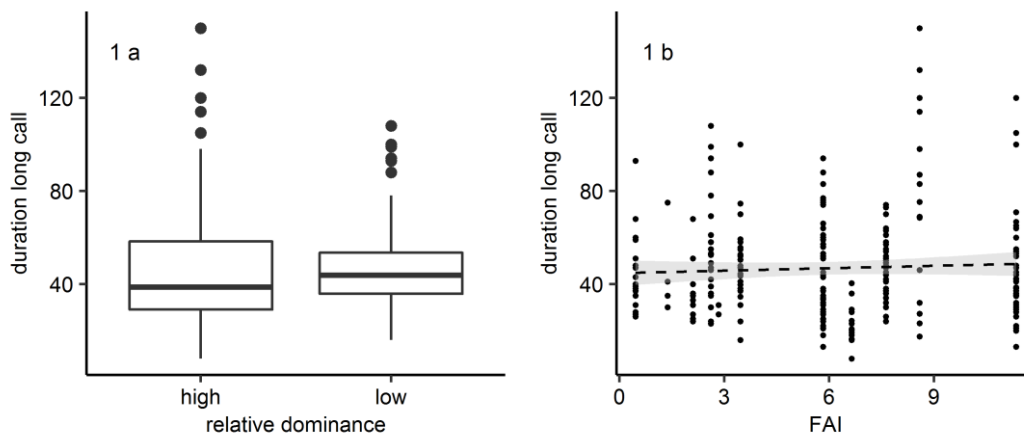


Figure 1a and 1b: The duration of long calls is not affected by the caller's relative dominance status (1a) nor is not affected by fruit availability (1b)

Impact of poor social knowledge

We found a significant relationship between the type of agonistic encounters and whether the dyad involved residents or visitors ($\chi^2_{(2)} = 6.372$, $P = 0.041$, $N = 16$). As the information on a rival's fighting ability becomes less perfect, physical fights become more likely (figure 2). We found the same relationship when we test over the course of eight years focal follow data ($\chi^2_{(2)} = 8.966$, $P = 0.013$, $N = 49$).

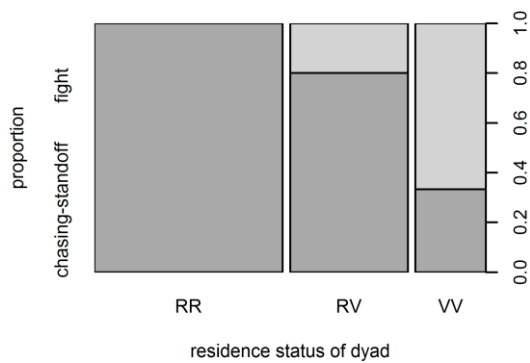


Figure 2: Relationship between dyad composition and intensity of agonistic encounters. The width of the bars is a reflection of sample size in each category.

Does long calling activity indicate fighting motivation?

Involvement in an agonistic encounter in a given months (yes/no) was predicted by an individual male's long call rates ($P = 0.006$, odds ratio = 1.102), using a binomial GLMM ($N = 362$) (see figure 3 and table 5).

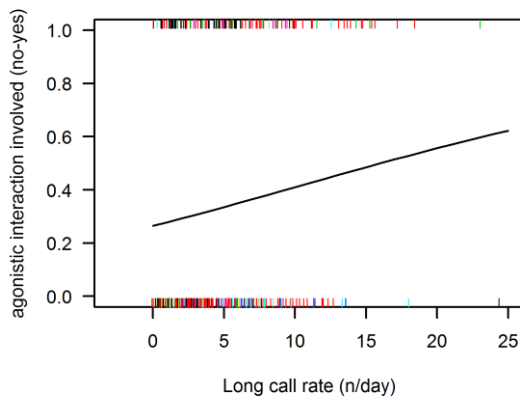


Figure 3: Probability of being involved in agonistic encounters as a function of the daily long call rate. The prediction line refers to the binomial GLMM prediction.

Table 5: The effect of long call rate on being involved in agonistic encounters. Parameter estimates, associated standard errors, and statistical significance as obtained from a binomial GLMM

Fixed effects	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.819	0.758	-2.401	
Long call rate	0.097	0.035	2.768	0.006

$\chi^2_{LRT(1)} = 8.159$, $P = 0.004$

Likewise, using a binomial GLMM ($N = 362$), we found that being a responder or not in a given month significantly predicted whether an individual was involved in agonistic encounters ($P = 0.047$, odds ratio=2.33)(see figure 4 and table 6). Additionally, in more than 70 % of the agonistic encounters the winner was also the individual that approached a rival (expected 50%). In the remaining encounters we were not able to disentangle who approached whom.

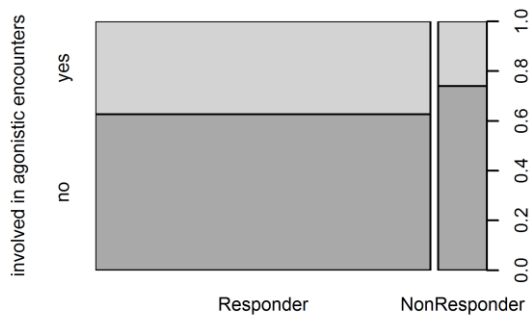


Figure 4: Probability to be involved in agonistic interactions as a function of being a responder or a non-responder. The width of the bars is a reflection of sample size in the two categories.

Table 6: The effect of being a responder or a non-responder on the involvement in agonistic encounters. Parameter estimates, associated standard errors, and statistical significance as obtained from a binomial GLMM

Fixed effects	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.114	0.850	-1.311	
Responder vs. non-responder	0.848	0.427	1.986	0.047
$\chi^2_{LRT}(1) = 3.893$, $P=0.048$				

Fluctuation of individuals' long call activity

Using a GLMM with poisson distribution ($\chi^2_{LRT(72)} = 363.73$, $P < 0.001$, $N=362$), we found that long call rates (mean= 4.60 per day, s.d. = 3.23) varied among the 10 individuals sampled ($\chi^2_{(9)} = 85.211$, $p < 0.001$), and also varied between the 10 months of ALS recording ($\chi^2_{(9)} = 66.393$, $p < 0.001$), as expected. More importantly, however individuals varied their calling rates across months (interaction: month*individual: $\chi^2_{(54)} = 172.968$, $P < 0.001$) (figure 5).

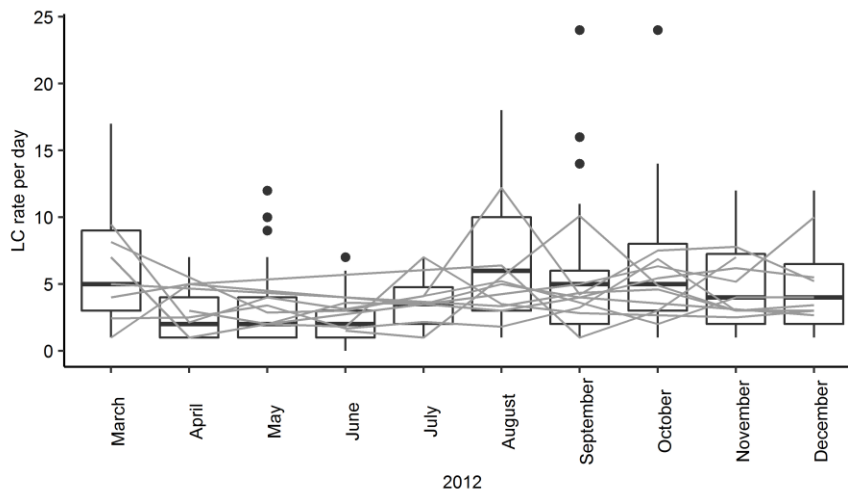


Figure 5: Variation of long call rates among individuals over a ten months period. Gray lines represent individuals.

Using a poisson GLMM (see table 7), we could show that long call rates per day (corrected for long calls given as response) were a good predictor of the long call response rate per day ($P < 0.001$).

Table 7: The effect of long call rate on long call response rate. Parameter estimates, associated standard errors, and statistical significance as obtained from a poisson GLMM

Fixed effects	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.075	0.146	-7.346	
Long call rate	0.112	0.015	7.418	<0.001
$\chi^2_{LRT(1)} = 45.079, P < 0.001$				

Using a generalized linear mixed model with a binomial distribution, we found that the difference of Elo scores established through long call interactions (delta Elo) between individuals involved in an agonistic encounter predicted the outcome (winner – loser) of agonistic encounters ($P = 0.039$, $N_{(chase, fight)} = 16$) (see table 9). Visitors were involved in 3 out of 4 out of 16 agonistic in which an individual with lower Elo score was the winner.

Table 9: The effect of delta Elo on the outcome of agonistic encounters. Parameter estimates, associated standard errors, and statistical significance as obtained from a binomial GLMM

Fixed effects	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.010	0.390	-0.025	
Delta Elo	0.009	0.004	2.063	0.039
$\chi^2_{LRT(1)} = 6.399, P = 0.011$				

During the ALS period 16 agonistic encounters (chases or fights) were observed during focal follows. Nine out of a total of 16 followed males were involved in agonistic encounters during the ALS period (3 residents and 6 visitors). The remaining 7 males that were never observed in agonistic encounters consisted of 2 resident males and 5 visitors (including the 2 non-calling post prime males). The majority of agonistic encounters were chases, but 3 were actual physical fights. All included the new male Chili (interestingly in all of these fights, one of the flanged males was mate-guarding a female). Two males got injured during fights: one was a resident Wodan (toe) and the other another visitor also first seen in 2012, Helium (face). Additionally, we found Chili with new injuries in the face in October (not followed for 3 days, fight must have happened during this time). We examined these three injured individuals in detail with Wilcoxon rank-sum tests. In the case of Wodan's injury, his long-call rates in the month before injury (Mdn = 13/day) were significantly higher than those in the month after the injury (Mdn = 4/day), $W = 130.5$, $P < 0.001$, $r = -0.764$ (large effect). For long-call response rates we also found a significant difference between the month before the injury (Mdn = 1/day) and after the injury (Mdn = 0/day), $W = 100.0$, $P = 0.036$, $r = -0.427$ (medium effect). Helium's (a new male that moved into the area) long call rates in the month before injury (Mdn = 8.6/day) were also significantly higher than in the month after the injury (Mdn = 6.2/day), $W = 69.5$, $P = 0.048$, $r = -0.452$ (medium effect). For long call response rates, we also saw a decline, from before the injury (Mdn = 2/day) to the months after the injury (Mdn = 0/day), $W = 69.0$, $P = 0.046$, $r = -0.456$ (medium effect). Finally, Chili, moved into the area at the end of July 2012. Chili was involved in 8 out of 14 observed agonistic encounters (5 wins, 3 defeats) during his presence. In October he was found injured in the face (scars and scratches all over it). Because he was found mate-guarding a female (Juni), it seems to be evident that he won the unobserved fight that must have happened a day before encounter according to focal follow data of Chili. But neither his long call rate nor his response rate showed a significant difference between the month before and after the fight with obtained injuries.

Discussion

An earlier study had shown that Bornean flanged male orangutans converge in an area dependent on fruit abundance and engage in long calling and responding to others' long calls dependent on the presence of sexually active females (Spillmann et al. 2017). We

concluded that males engaged in confrontational assessment. However, these results held for the average male and may have masked important variability in the behavior of individual males, because males have highly variable social knowledge of their rivals' fighting ability and show considerable fluctuations in their own fighting ability. Here, we tested this suggestion with data on individual males, using a combination of focal follow data and data stemming from an acoustic localization system (ALS), which provided us with a comprehensive record of call activity and male presence in the area over a period of 10 months in 2012.

We first tested whether the presence of sexually attractive females did predict long call activity on an individual level as already found on an aggregate level in a recent study (Spillmann et al., 2017), and found the same effect of sexually attractive females on an individual level. This is an important result, because it suggests that males do not have much information on when and where females are sexually receptive, and thus concentrate their search for females in areas of high fruit abundance (Spillmann et al., 2017).

A key assumption of the confrontational assessment model is that long calls do not act as costly signals that indicate absolute fighting ability. If they did, males would not need to approach and confront each other to assess their relative fighting abilities. We found that producing long calls was not energetically costly: they were produced at a low rate (mean= 4.60 per day, s.d. = 3.23) and were relative short (mean= 46.73 sec, s.d. = 22.45), and neither rate of calling nor call duration was affected by local fruit abundance (and thus energy inputs). Moreover, long call duration was not affected by a male's relative dominance status. Thus, producing long calls is not unusually energetically costly compared to other systems where only high ranking individuals can bear the cost to produce relative long lasting and exhausting calls as e. g. in red deer roars (Clutton-Brock and Albon, 1979b), or in sage grouse (Vehrencamp et al., 1989). This conclusion is also supported by the observation that male orangutans can increase their call rates several-fold when necessary. For instance, after a playback experiment using a long call from an unfamiliar male, a resident male approached the location of the experiment from an estimated distance of about 700-800 m uttering more than 20 long calls during the subsequent time period of 6.5 hours (BS, unpublished data).

Males therefore can extract a rival's individual identity from his long calls (if they know him), but not his actual fighting ability. The best they can do therefore is to indicate their fighting motivation in their long-calling activities. Indeed, we found that males more likely to commit to agonistic encounters increased long call rates, regardless of whether they won or lost a fight. We also found that males that responded to others' long calls were more likely to get involved in agonistic interactions. As expected by these results, we found that fluctuation in fighting motivation is reflected in long calling and responding activity. However, agonistic encounters were also affected by social knowledge. Physical fights involved always at least one visitor in the interacting dyad, indicating that males who knew each other were far less likely to get involved in escalated contests, even if they came close to assess each other's fighting ability. These results are an indication that agonistic encounters are an escalation between individuals where fighting motivation is high and proper assessment of fighting ability had not yet happened. Figure 6 provides a summary of these results in the form of a decision tree followed by a male as a function of his fighting motivation.

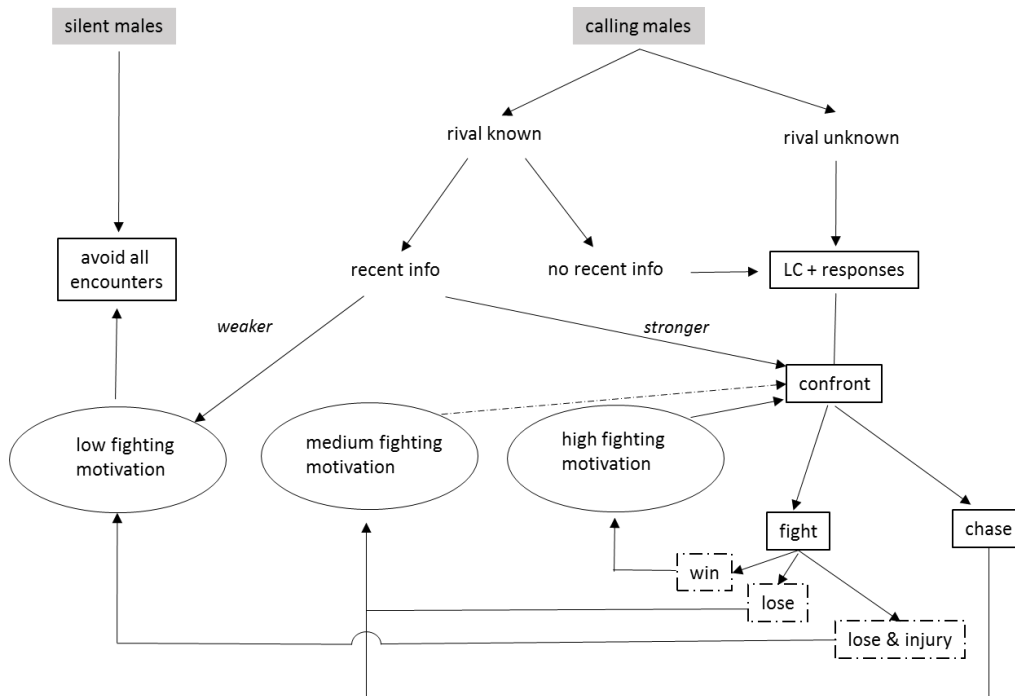


Figure 6: Flow chart of decision making depending on social knowledge and fighting motivation as the driving force in the competitive regime of Bornean flanged male orangutans.

We now use additional information to evaluate the correctness of the decision tree. First, we need to distinguish between calling and non-calling males. Post-prime males seemed to cease calling altogether and therefore avoid contest competition (see figure 6; silent males). During our ALS period one flanged male with shrunken cheek flanges never called and this non-calling behavior was persistent in all following years during focal follows (2013, 2015, and 2016). Another male also did not call, even though his physical appearance did not betray this, but he must be rather old because he was in 2007 already estimated as old.

We suggest that calling males must also adjust their calling behavior in relation to their fighting motivation. Therefore, in a first step identification of a caller might be most important upon hearing a long call of a rival. When the caller is known and social knowledge is up to date the receiver will usually act according to his knowledge about his own relative fighting ability in relation to the rival. This confirms that a male's decision making is improved when he has information, such as the rival's identity, that can predict the outcome of a possible agonistic interaction (Dall et al., 2005, Arnott and Elwood, 2009). However, information acquired through social recognition needs to be reasonably stable (Bergman and Sheehan, 2013), which is not always the case in orangutans, especially among males that did not meet for a long time. Therefore, only resident males that have updated social knowledge of each other can rely on individual recognition to assess each other and decide how to react upon hearing a rival's long call. If the caller is unknown or the social knowledge is outdated, social recognition and knowledge alone, even though important in non-human primate species, does not suffice to assess rivals in Bornean males. In this setting the decision making of the receiver will depend more on his own fighting motivation than on assessment of his rival's fighting ability. Assessment of a rival male according to long call activity alone is not perfect, since long calls are not costly to produce and do not reveal a male's absolute fighting ability. Nevertheless, a calling male risks being attacked by a rival, so the decision to engage in increased calling activity may be driven by contest motivation. Hence, males with high fighting motivation call and respond more frequently, but run the risk of getting injured, whereas males with low fighting motivation call and respond less and thereby are able to avoid agonistic encounters (see figure 6).

Once a male is involved in agonistic encounters, factors as winning, losing, and losing with injuries impact his future calling behavior. Thus, a healthy male in good

condition calls and responds more than an injured male or one in poor condition (Steenbeek et al., 1999, Erb, 2012). In the presence of sexually attractive females, males' decisions are more likely to be escalatory, as reflected in the increased observation of agonistic encounters during the months with sexually attractive females present. Over time, such competitive interactions may sap a male's strength or motivation, because mate guarding is energetically demanding (van Schaik, 1999, Utami et al., 2002). The observed variation in calling and responding activity over time could reflect such processes. In addition, we found a tendency that mate-guarding males were more likely to engage in physical fights (B.S. unpubl. data). This may have two reasons: (i) a male's motivation to compete over a highly valuable resource is increased, since we found higher call activity when sexually attractive females are present; and (ii) consorting females may actively provoke agonistic encounters between a mate-guarding male and another calling male by approaching the latter (pers. observation) (Cox and Le Boeuf, 1977, Fox, 2002).

Males that lost fights did not necessarily modify their calling activity. However, we were able to show a decrease in long-calling activity for two males after losing and suffering an injury.

In conclusion, this study shows that Bornean flanged males indeed show an unstable form of contest competition, described by the label "confrontational assessment", especially during periods with sexually attractive females present. The intensity of competition is related to the imperfect knowledge of rivals' fighting ability, due to the high local turnover of flanged males. Current fighting motivation is reflected in a male's calling behavior, which fluctuates considerably over time. Their decision to invest in contest or not is best explained with contest motivation. Future work should examine whether a correlation between testosterone levels and calling behavior exists. If so, there may be a parallel between the Bornean male orangutans' confrontational assessment and the musth system of elephants (Poole et al., 2011).

The importance of using an ALS

The ALS approach was essential to test confrontational assessment on the individual level as well as the hypothesis that long calls indicate contest motivation. Individual focal follow data is too scattered to address this kind of questions. In table 10

we compiled all tested predictions with the ALS data and introduce the feasibility of testing these predictions with data from focal follows (2005-2012) collected at Tuanan field site. Table 10 shows that the long-term follow data generally lacked power, although their results tended to go in the same direction as the ALS data (3 of 9 times significantly so; more details see supplementary material III). We conclude that a social mating system with widely dispersed individuals, such as that of orangutans, makes this kind of analyses almost impossible without an ALS, because it is impossible to establish the presence of males in the area and their calling behavior on a daily basis with traditional focal follows alone. The only option to conduct such a project would be either to have numerous observers simultaneously follow most of the males in the area, which is logistically difficult, or to capture all males and fit them with GPS collars, which is legally impossible.

Table 10: Comparison of the feasibility to test predictions between data collected via ALS and focal follow data

	ALS	Focal follow data
I Validation of confrontational assessment on an individual level		
Long call rate increases with the presence of sexually attractive females	yes	yes
Response proportion increases with the presence of sexually attractive females	yes	model not significantly different from the null model
Being a responder is influenced by the presence of sexually attractive females	yes	model not significantly different from the null model
III testing the hypothesis that long calling activity reflects contest motivation		
An individual's involvement in agonistic encounters is predicted by its long call rate	yes	model not significantly different from the null model
An individual's involvement in agonistic encounters is predicted by being a responder	yes	model not significantly different
II Fluctuation in fighting ability reflected in long calling activity		
Individuals' call rate vary among individuals and over time but not for all individuals in the same direction	yes	yes
Individuals with high call rate show high responding rate	yes	yes
Long call responses predict the winner and loser of an agonistic encounter	yes	not possible (usually only data of one individual available)
An injured individual decreases long call rate and response rate	yes	not enough data usually for losers after an agonistic encounter

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Conclusion and perspectives

The aim of this thesis was to shed light on a sexually selected trait: the orangutan long call. I was primarily interested in the underlying competition mechanism, in particular how orangutan flanged males assess each other's fighting ability through this long-distance communication system. Even though several researchers had studied this long-distance signaling system before, there were still several unsolved questions and conflicting opinions regarding the underlying functions of long calls. Some suggested the orangutan long call merely functions in male spacing (Mitani, 1985), whereas others highlighted the mate attraction and female protection functions (Delgado, 2003, Mitra Setia and van Schaik, 2007). Not surprisingly, the mate attraction and female protection functions were confirmed in the more gregarious Sumatran orangutans where a dominant flanged male in the area is present. Bornean orangutans are less gregarious and it is difficult to assess which male is dominant, probably due to the higher proportion of flanged males present in an area compared to unflanged males because of the absence of developmental arrest (Utami et al., 2002, Pradhan et al., 2012, Dunkel et al., 2013). Accordingly, the often observed earshot-association in Sumatran females, in which the locally dominant flanged male serves to protect females from sexual harassment by unflanged males and probably from infanticide (Fox, 2002, Delgado, 2003, Mitra Setia and van Schaik, 2007), was not found in Bornean orangutans although some indications for a mate attraction function were given (Spillmann et al., 2010).

Traditional individual focal follow data have so far not been able to resolve these issues. Moreover, the alternative – to track individuals in time and space with GPS transmitters and (Tomkiewicz et al., 2010), if acoustic data is needed, combined with an integrated microphone and recorder – is not allowed in wild orangutans, because of the difficulty and risk of capturing individuals and the disturbance that accompanies such an approach. Therefore, acoustic tracking of vocalizing animals is the best available option, so I decided to develop a new methodological approach to improve data collection that produces a comprehensive data set with information about male presence in a study area and their long call activity over time and space. In chapters 1 and 3, I presented an approach to collect data with a passive acoustic monitoring system, in particular an acoustic localization system (ALS), and an automated caller recognition procedure that enables to identify long calls recorded by the recorder grid. This approach has a long history in marine mammals, in particular in cetaceans (Watkins and Schevill, 1972). Although acoustic location of terrestrial animals became more recognized through studies

of communication networks in several avian studies (Peake et al., 2001, Mennill and Vehrencamp, 2008), studies in terrestrial mammals are still scarce (Collier et al., 2010, Thompson et al., 2010, Wrege et al., 2012). And in non-human primates passive acoustic monitoring has so far been established only in two species: orangutans (this study with additional acoustic localization) and chimpanzees (Piel, 2014, Kalan et al., 2016).

In chapter 1, I validated the procedure of long call extraction and acoustic localization of acoustic data collected through a recorder grid consisting of 20 recorders in a 300 ha area with 500 m inter-recorder distances. The recorders were equipped with a GPS sensor that allowed for the relevant time synchronization of the sound files. A trained recognition algorithm extracted long calls reliably for distances up to 700 m from a recorder. I found that the acoustic coverage spanned an area of around 900 ha, and that acoustic localization was accurate in an area of 450 ha.

The extracted long call data from ALS was used to examine intra-sexual competition mechanisms in Bornean flanged males (chapter 2). Orangutans are semi-solitary and their mating system is described as promiscuous with roving males (van Schaik and van Hooff, 1996). Hence males range widely in search of fertile females. Orangutan females do not broadcast their reproductive state as many other non-human primates do (Knott, 2001). In such a system, males can pursue different competitive strategies. I used the ALS data to disentangle whether components of scramble and contest competition are present in Bornean males. This data allowed me to estimate the number of males present in an area and revealed the call activity of all these males in time. I was able to show that the *presence* of flanged males in an area was a function of local fruit availability, whereas their calling behavior was determined by the number of sexually attractive females and the number of rival males present. The latter two factors also predicted the males' tendency to respond to rivals' long calls and the proportion of males that engaged in such responses. Therefore, males are attracted to areas with high local fruit abundance and once there adjust their calling behavior to the presence of fertile females and rival males. Thus, dominant males cannot keep other males from coming into an area, suggesting scramble competition, but flanged males increased advertising and assessment of a rival's fighting ability whenever sexually attractive females were present, indicating contest. This mixed competition mechanism was called "confrontational assessment" because of the highly variable social knowledge: because new males or males not met for a while move into the area, assessment of a rival's fighting ability is deficient,

and needs to be updated by an actual encounter, sometimes to the point of physically fighting.

This conclusion was drawn at an aggregate level, but a proper test of “confrontational assessment” required observations on an individual level (chapter 4). Before this was possible, a methodological approach was needed to identify long calls recorded by the ALS. In chapter 3, I therefore tested the accuracy for orangutans of a caller recognition procedure originally developed for human speaker recognition. This automated approach uses mel-frequency cepstral coefficients (MFCC) feature extraction. This cepstral representation captures the vocal tract resonances of a caller, and is based on the source-filter model of human speech production (Davis and Mermelstein, 1980). Subsequently, these MFCCs were modelled using a GMM-UBM (a gaussian mixture model with universal background model) framework for individual identification (Sadjadi et al., 2013). The UBM is a universal background model that is trained on a subset of data from a number of callers. The accuracy of correct identification for high-quality recordings collected during individual focal follows was 93.3% for 14 individuals. It was 72.2% for recordings stemming from the ALS, with its variable microphone-caller distances (20-420 m). These results supported the feasibility of an automated caller recognition procedure for acoustic data collected through an ALS.

Having found that the intra-sexual competition mechanism was identified as a combination of scramble and contest components (confrontational assessment) it became crucial to understand how flanged males assess relative fighting ability in contests. Usually measurements to capture dominance relations reflect the dyadic dominance relationship between contestants (Drews, 1993). But in a species where social context is rather unstable, as in the Bornean orangutan where males are solitary and roam widely and often have no or only outdated information about rivals’ fighting ability, assessment of their own fighting ability relative to rivals is necessary. In such a shifting social context a trait that enables to reduce risky and costly fights would be advantageous (Grafen, 1990, Johnstone and Norris, 1993, Maynard Smith and Harper, 2003).

An obvious possibility is that acoustic features of a male’s long call correlate with fighting ability (Fischer et al., 2004). However, in a preliminary study I found no significant discrimination in the acoustic structure of a male between periods when he appeared rather dominant compared to when he seemed rather subordinate (BS unpublished data). Additionally, I could confirm Delgado’s (2006) finding that long call

production is not costly. In particular, we found no difference in call duration between relative high ranking and low ranking individuals, and fruit abundance had no effect neither on call duration and call rates. As found in the second chapter the presence of sexually attractive females was the best predictor for individual's call and response activity.

I therefore focused in chapter 4 on the possibility that the long call, a secondary sexual characteristic (Delgado, 2006) is an indicator of individual's fighting motivation in respect of their call and response activity. Even though males would benefit from an honest signal that broadcasts absolute fighting ability, long calls do not. They rather act as conventional signals where production cost is low but increased calling behavior bears social cost (Vehrencamp, 2000, Laidre and Johnstone, 2013), and convey information about short-term changes in motivation (Rubenstein and Hack, 1992, Vehrencamp, 2000). Uncertainty about rivals' fighting ability is most pronounced in males that either never met before or had not met for a while. This lack of information was reflected in a relationship between the intensity of agonistic encounters (chase versus fight) and the competing males' residence status (resident versus visitor).

I could also show that an individual's involvement in agonistic encounters independent whether he won or lost a fight was a function of an individual's call rate and his tendency to respond to others' long calls. Finally, I found that fluctuation in fighting motivation is reflected in long-calling and responding activity. Hence, males with high fighting motivation call and respond more frequently, but run the risk of getting injured, whereas males with low fighting motivation call and respond less and thereby are able to avoid agonistic encounters. Factors as winning, losing, and losing with injuries also impact their future calling behavior (see chapter 4, figure 6). Nevertheless, individuals will adjust their calling behavior in respect to the current social environment and available valuable resources, and a healthy male in good condition calls and responds more than an injured male or one in poor condition (Steenbeek et al., 1999, Erb, 2012).

In conclusion, this study shows that Bornean flanged males indeed show an unstable form of contest competition where confrontation of rival males is necessary especially during periods when contest motivation is increased due to the presence of sexually attractive females.

The benefit of an ALS can be enormous, especially when comprehensive data collection of all members of a group or in widely dispersed solitary animals is not possible with standard procedures. However, to examine an animal's social system such data is generally required. This thesis demonstrates the advantage of this methodological approach because almost all addressed questions in the behavioral part (chapter 2 and 4) could not have been tested in such detail without the additional data collected through the (ALS).

The behavioral part of this thesis (chapter 2 and 4) contribute to the understanding of the orangutan's social system and show the importance of a long-distance communication system in their intra-sexual competition mechanism, but also the use of this secondary sexual characteristic in a species with widely distributed individuals the Bornean orangutan.

Perspectives

I can imagine that passive acoustic monitoring, with or without acoustic localization of callers, could become more popular if the labor-intense data extraction could be made more efficient through automated approaches, as already mentioned in the thesis' general introduction (addition to chapter 1). Passive acoustic monitoring can be beneficial for an array of research questions in conservation or behavioral biology, especially in species that conspicuously vocalize but are difficult to observe directly (Wrege et al., 2012), in species with fission-fusion societies where a group is usually divided into subgroups (e.g. chimpanzees; (Kalan et al., 2016), or where tracking individuals with GPS transmitters is impossible. However, an acoustic localization system requires thorough planning beforehand to avoid unpleasant surprises in the field as well as elaborate data management afterwards (chapter 1).

I concentrated in this thesis on male-male competition through the orangutan males' long distance signal. But other questions, such as inter-sexual interactions can also be addressed in future using the same approach. With a better knowledge of locations and calling activity of individual males in space and time, female reactions, particularly their ranging decisions, can be analyzed in more detail. This is particularly important since the female attraction or male protection function in Bornean orangutans has not yet been definitely assessed.

Bornean and Sumatran orangutans differ in many aspects, from morphology and socio-ecology to cognition (Delgado and van Schaik, 2000, Wich et al., 2009). The ALS approach provides a crucial tool to make a systematic comparison of intra-sexual and inter-sexual interactions and the males' dominance relations between the two species in order to disentangle the many unresolved questions.

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Validation of an acoustic location system to monitor Bornean orangutan (*Pongo pygmaeus wurmbii*) long calls

I Recorder and power supply

The installation of the 20 recorders in the forest took around one week. The most challenging part was to find open locations for the solar panels. Sometimes we had to install them on tree tops.



Figure 1: Autonomous recorder powered by external dry gel battery covered through a waterproof case. A solar panel charged the dry gel battery continuously.

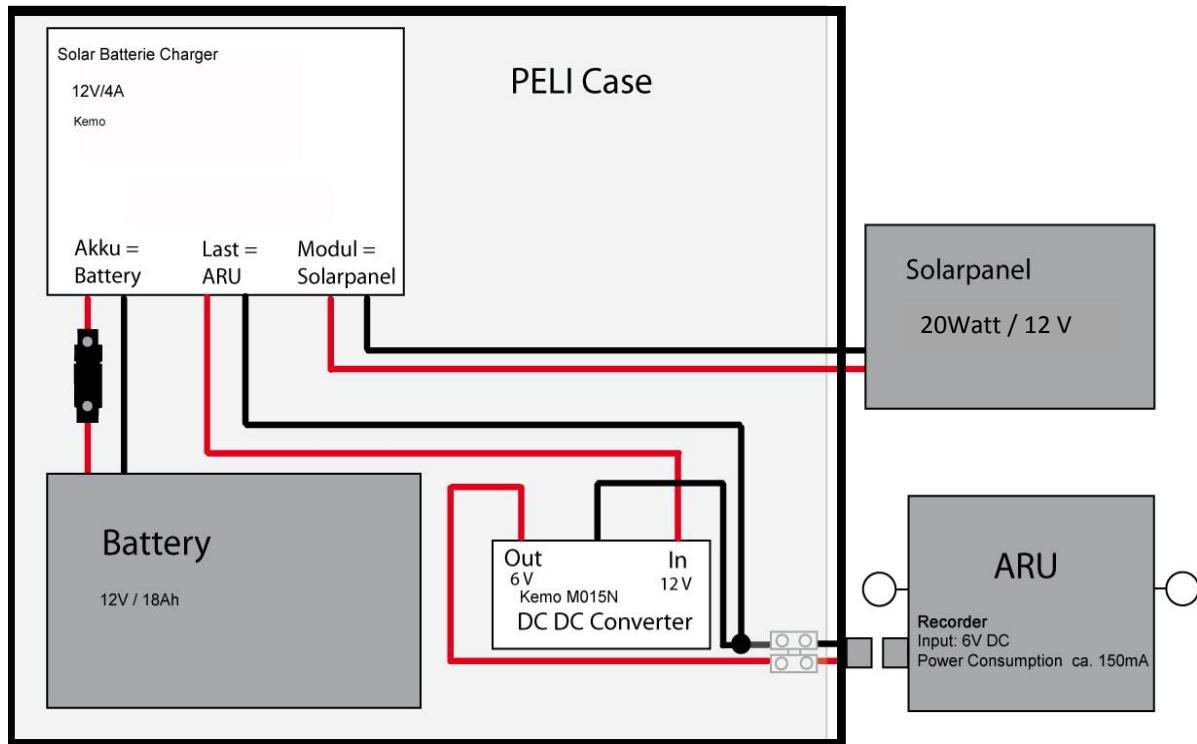


Figure 2: Scheme of power supply of the autonomous recorders. Solar panel (20 Watt) charges via solar charger dry gel battery (12V/18Ah) and via DCDC converter that transforms 12 V into 6 V to power the recorder.



Figure 3: Damages on material mostly occurred through animals that gnawed on parts of the installation.

II Study area covered with recorder grid (ALS)

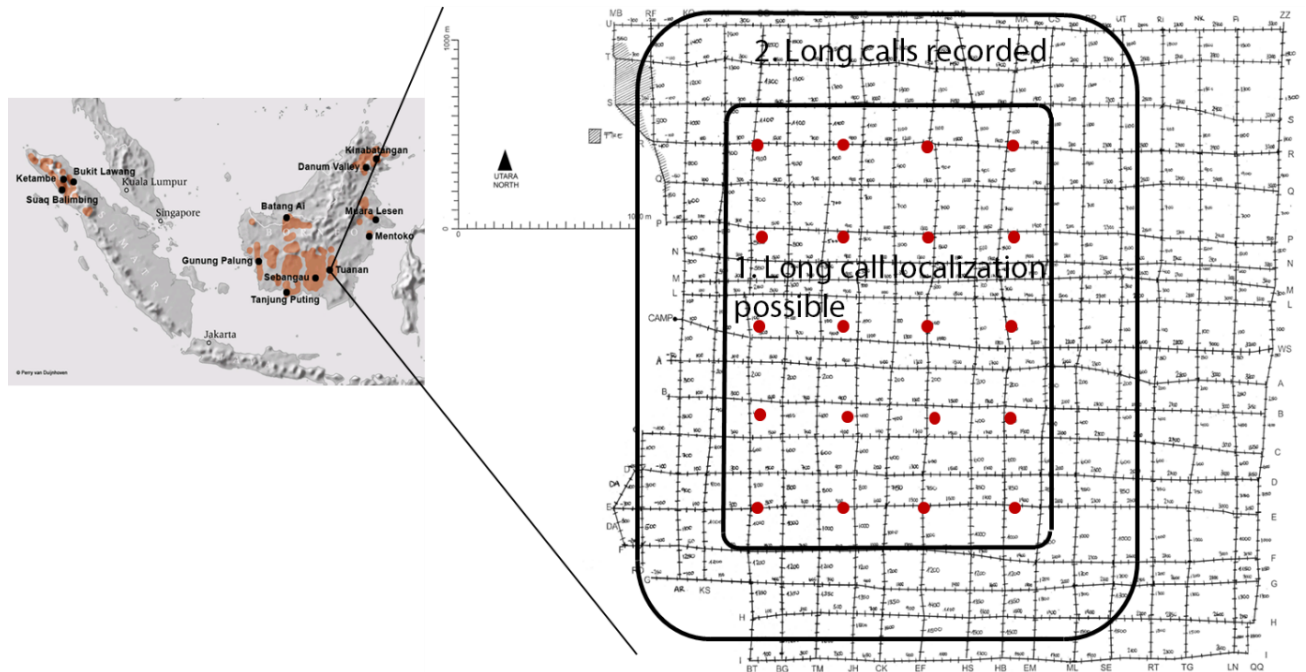


Figure 4: Recorder array in study area with the area where localization is possible and the maximal area where long calls were reliably recognized through the detection algorithm.

Confrontational assessment in the roving male promiscuity mating system of the Bornean orangutan

I Empirical validation of the use of ALS as a proxy for male presence

Percentage of individual focal follow days with and without long calls

In order to capture all males by the ALS method, flanged males need to give a long call at least once a day. In order to control how many males meet this requirement, we counted long call occurrences of flanged male individual focal follow days (observation time > 5 hours/day, total observation time > 35 hours per individual) in order to establish the likelihood of giving at least one long call for each individual per day. In total we observed 16 different flanged males ranging in the study area during the sampling period of ALS (March-December 2012). On 11 of them we collected > 35 hours of observation time (total observation time 1200 hours). One flanged male never called during individual focal follows (a male with shrunk cheek pads, probably post-prime: Knott et al. 2010), but the other ten males called on 93.8 % of the observation days (see figure 1). This result suggests that the measure of counting calling males per day with the ALS method is justified because all non-senescent (around 90%) flanged males call during most focal follow days. The only male that ceased calling (post prime male Fugit) over longer periods no longer played an important role in the system.

Long call rate/hour

Flanged males usually call (see above), and therefore we assume that males are equally likely to call at all times, but if males change their calling behavior in response to fruit availability, this assumption is violated. We fitted a Generalized Linear Mixed Effects Model (GLMM) to data collected observationally during focal follow days. Each male's average long call rate per hour ($\ln(\text{long call rate/hour})$) was examined as a function of food availability, the number of sexually attractive females and the focal male's estimated dominance status (either being high or low), controlling for repeated measurements on each male. The estimated dominance rank was established by assigning males with a high dominance rank to a class of males that initiated chases and

fights, whereas males that were rather passive or never participated in competitive interactions were assigned to a low-dominance class.

The GLMM model was significant $\chi^2_{\text{LRT}} = 171.34$, $p < 0.001$. We found that individual long call rate/hour is best explained by the estimated dominance class (high-low) of the individuals ($B=0.161$, $\text{s.e.} = 0.059$, $t\text{-value}=2.711$, $P=0.018$, $N=164$ of 16 individuals), and that neither fruit availability nor the number of sexually attractive females had an effect. Thus the ALS' assumption was validated in respect that fruit availability had no effect.

Reference

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II Latency of long call responses

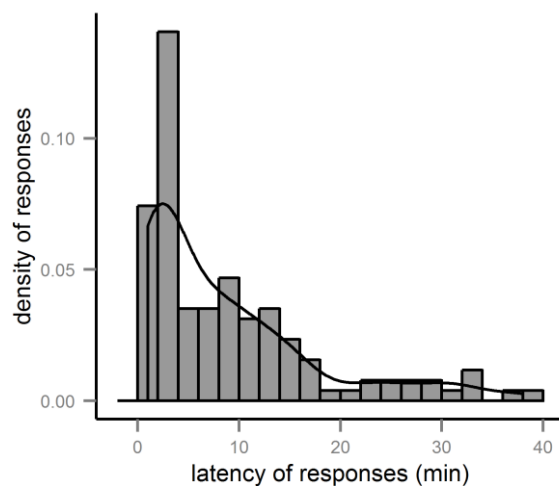


Figure 1: Density distribution of long call responses as a function of the latency. Immediate responses occur with a latency < 5 minutes

Long calls as indicators of contest motivation

I Focal follow data

Predictions tested with individual focal follow data

The focal follow data is limited because it lacks detailed information on the presence and locality of other flanged males than the followed individual. Additionally, we fairly systematically lose the losers of agonistic encounters as focal individuals, and thus have no data. This is contrary to winners that usually keep calling and are therefore found again, in case we lose them. But importantly individual focal follow data contains detailed data on social behavior.

Methods

The data of individual focal follows stem from data collected from 2005 to 2012. Long call behavior of flanged males was extracted from 6035 hours of individual focal follow data ($N = 20$). Focal follows for a given male were included if focal follows with observation duration > 6 hours per day summed up to a total of at least 75 hours in the period 2005 -2012. We calculated mean monthly long call rates/hour for each male that was included in the dataset.

Statistics

We fitted a model to assess which social (male's residence status, presence of sexually attractive females) or ecological (monthly fruit availability) variables (fixed effects) best predicted aspects of individual monthly mean call rate per hour. All following models included individuals as random effect. We fitted a linear mixed model (LMM) for individual mean monthly call rates.

We fitted a linear mixed effect model LMM (focal follow data = LC rate per month) as response variable and individuals, time period (focal follow data = quarter years), and the interaction between individual and time period as predictors. We introduced individuals as random effect.

In order to find whether long call rate per month is a good predictor of long call response rate we fitted a linear mixed effect model with individuals introduced as random effect.

Results

Confrontational assessment on individual level

A significant linear mixed model ($\chi^2_{\text{LRT}(3)} = 9.361$, $P=0.025$) showed that the presence of sexually attractive females is a good predictor for mean long call rates per month of individual males ($B = 0.086$, $SE = 0.038$, $t \text{ value}_{(181.4)} = 2.261$, $P = 0.028$). Also here, neither male's residence status (resident versus visitor) nor fruit availability had an effect on individual long call rates.

Is fluctuation of individuals' relative fighting ability reflected in long call activity?

A significant LMM ($\chi^2_{\text{LRT}(131)} = 429.77$, $P < 0.001$, $N=195$) found a tendency towards significance in the variation of long call rates among 20 individuals ($\chi^2_{(19)} = 28.565$, $P = 0.073$). Mean monthly long call rates varied over the 31 quarter-years ($\chi^2_{(30)} = 113.438$, $p < 0.001$). And also here, individuals varied their calling rates across quarters ($\chi^2_{(82)} = 267.824$, $p < 0.001$ (interaction: quarter*individual)).

Table 1: Using a LMM, we could show that individual long call rates per month were a good predictor of the long call response rate per month ($P < 0.001$).

Fixed effects	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	0.002	0.004	0.509	
Long call rate	0.030	0.006	4.784	<0.001
$\chi^2_{\text{LRT}(1)} = 21.825$, $P < 0.001$				

II Identification of long calling males from the ALS

Whenever possible we cross-checked different identification components to assign a long call to an individual (see table below).

Table 1: Compilation of the identification components used

Main type of data used for identification	components used for identification	% identified of all identified calls
Focal Follow Data involved	F	14.07
	F & CR (min. chance 0.8 to be correct)	1.37
	CR & TDR & F	1.70
	F & CR & Idio	0.07
	CR & Idio & TDR & F	2.09
	Idio & TDR & F	0.46
	TDR & F	3.27
Caller Recognition	CR	1.76
	CR & idio	9.30
	CR & TDR	5.24
	CR & idio & TDR	10.21
Idiosyncrasies	Idio & TDR	22.97
	Idio	5.37
Td-Rule but derived former identifications through caller recognition or idiosyncrasy	TDR	22.12

F=focal follow; CR= caller recognition; Idio=idiosyncrasies; TDR= time-distance rule

III Residents versus visitors

Here, we examined the duration of individual males' presence in the study area. The data included focal follow data and mere encounters with flanged males in the area. We compiled the data per year to show how long (in months) individual males (N=39) were present per year over an eight year period (see figure 1). A male that was present < 6 months belonged to the visitor group.

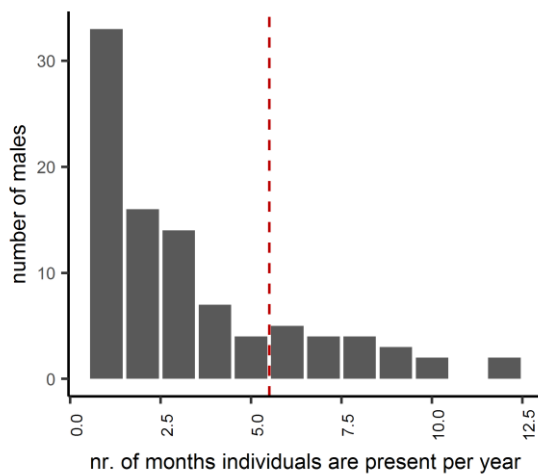


Figure 1: The number of month individual males were present during a year over an eight years period. The break-point of being visitor or resident is 6 months (resident ≥ 6 months present in the area)

But males do not only stick to one residence status, they can rather switch between them. A male switches either from resident to visitor when he was not seen for at least 12 continuous months, or from visitor to resident when he was seen for ≥ 6 months in a year. In this case we labeled him as resident after the fourth month of encounter.

Curriculum Vitae

Surname	Spillmann
First name	Brigitte
Date of birth:	20-06-1971
Nationality:	Swiss

Academic Education

2011 - 2017	PhD Evolutionary Biology (Natural Science), University of Zurich, Department of Anthropology. Dissertation: Long calls mediate male-male competition in Bornean orangutans: an approach using automated acoustic localization
2008	MSc Evolutionary Anthropology, University of Zurich, Department of Anthropology. Thesis: Females' reaction to context dependent long calls of flanged males in Bornean orangtuans (<i>Pongo pygmaeus wurmbii</i>)
2007	BSc Bachelor of Science in Biology, University of Zurich

Research experience

2011 – 2013	Fieldwork in South Aceh (Suaq Balimbing) and Central Kalimantan (Tuanan), Indonesia
March – Sept 10	In the framework of the cooperative breeding hypothesis: Leading a group service experiment with Gibbons at the Leintalzoö in Germany and supporting the practical part of a master's thesis project: group service experiment with chimpanzees at the Leintalzoö in Germany
Jan. – Feb. 09 and Oct. – Dec. 09	Data entry and GIS (Geographic information system) analyses at the Anthropological Institute and Museum Zurich, Switzerland
2008	Master thesis: analyses of the acoustic structure in long calls, analyses of behavioral data, and analyses of playback experiments
2007	6 month fieldwork for my master's thesis at the Tuanan field site, Central Kalimantan, Indonesia

Grants awarded

2011	The Leakey Foundation, USA, Research Grant
2011	Basler Stiftung für biologische Forschung, Switzerland, Research Grant
2011	Stiftung Dr. Joachim de Giacomini, Switzerland, Research Grant

External presentations

2017 15th Meeting Gesellschaft für Primatologie in Zurich, Poster presentation: „*Confrontational assessment*“ among Bornean orangutans (*Pongo pygmaeus wurmbii*) reflects instability in male dominance hierarchy

2016 26th Congress of the International Primatological Society in Chicago, *Who is calling today? Instability in male presence and dominance hierarchy among Bornean orangutans (Pongo pygmaeus wurmbii)*

2015 6th International Congress of the European Federation for Primatology in Rom, Determinants of Long Call Activity in Bornean Orangutans (*Pongo pygmaeus wurmbii*)

2014 25th Congress of the International Primatological Society in Hanoi, *Autonomous auditory monitoring (AAM) of Bornean orangutan long calls*

2013 5th International Congress of the European Federation for Primatology in Antwerp, *Who is calling out there?*

2013 10 years Tuanan, Universitas Nasional Jakarta, Indonesia, *What is the message transmitted by a long call?*

2011 Presentations at Universitas Syiah Kuala (Unsyiah), and Sekolah Tinggi Ilmu Kehutanan, Banda Aceh, Indonesia, *Research on the Asian great ape*

2009 3rd International congress of the European Federation for Primatology in Zurich, Poster presentation: *A new approach to long call function in Bornean orangutans*

2009 11th Meeting Gesellschaft für Primatologie in Hannover, *Context affects acoustic properties of long calls given by flanged male orangutans*

Peer reviewed publications

Piel, A.K., Spillmann, B., Höpfner, A., (in prep.) Calling in the dark: Nocturnal vocal behavior of wild chimpanzees and orangutans

Spillmann, B., Willems, E.P., van Noordwijk, A.M., Setia, T.M., van Schaik, C.P, (2017) Confrontational assessment in a roving male promiscuity mating system of the Bornean orangutan. Behavioural Ecology and Sociobiology:71,20

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Former Education and Work Experience

1998 – 2002	Confederate Maturity, AKAD Zurich, Switzerland (extra-occupational)
1991 – 2003	Occupations as medical technical assistant in doctor's surgeries and hospitals
1988 – 1991	Apprenticeship as medical technical assistant
1987 – 1988	One year diploma at commercial school

ARTICLE

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The evolutionary origin of human hyper-cooperation

J.M. Burkart¹, O. Allon², F. Amici³, C. Fichtel⁴, C. Finkenwirth¹, A. Heschl⁵, J. Huber⁶, K. Isler¹, Z.K. Kosonen¹, E. Martins¹, E.J. Meulman¹, R. Richiger¹, K. Rueth¹, B. Spillmann¹, S. Wiesendanger¹ & C.P. van Schaik¹

Proactive, that is, unsolicited, prosociality is a key component of our hyper-cooperation, which in turn has enabled the emergence of various uniquely human traits, including complex cognition, morality and cumulative culture and technology. However, the evolutionary foundation of the human prosocial sentiment remains poorly understood, largely because primate data from numerous, often incommensurable testing paradigms do not provide an adequate basis for formal tests of the various functional hypotheses. We therefore present the results of standardized prosociality experiments in 24 groups of 15 primate species, including humans. Extensive allomaternal care is by far the best predictor of interspecific variation in proactive prosociality. Proactive prosocial motivations therefore systematically arise whenever selection favours the evolution of cooperative breeding. Because the human data fit this general primate pattern, the adoption of cooperative breeding by our hominin ancestors also provides the most parsimonious explanation for the origin of human hyper-cooperation.

¹Anthropological Institute and Museum, University of Zurich, Winterthurerstrasse 190, 8057 Zürich, Switzerland. ²Institute of Cognitive and Evolutionary Anthropology, University of Oxford, 64 Banbury Road, Oxford OX2 6PN, UK. ³Department of Comparative and Developmental Psychology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany. ⁴Behavioral Ecology and Sociobiology, German Primate Center, Kellnerweg 4, 37077 Goettingen, Germany. ⁵Institute of Zoology, University of Graz, Universitätsplatz 2, 8010 Graz, Austria. ⁶Institute of Biology, University of Neuchâtel, Emile-Argand 11, 2000 Neuchâtel, Switzerland. Correspondence and requests for materials should be addressed to J.M.B. (email: Judith.Burkart@aim.uzh.ch).

Compared with other primates, including the other great apes, humans show extremely intensive cooperation, which is increasingly recognized as being ultimately responsible for our unusual cognition, technology and culture^{1–3}. A variety of mechanisms underlie this unusual level of cooperation. High social tolerance and reactive prosociality, as shown in empathy-based targeted helping where individuals respond to signs and signals of need by others, are clearly important⁴. But since these may also be found in other great apes^{5,6}, they are evidently not sufficient to support human-like cooperativeness. Some have instead argued that a proactively prosocial motivation, also called other-regarding preference, is the critical mechanism enabling human cooperation³. In proactive prosociality, individuals spontaneously assist others, for instance by provisioning, without direct gains for themselves and without being solicited. Recent years have seen a growing number of studies assessing proactive prosociality in nonhuman primates. Taken together, these studies^{5,6} revealed its presence in some nonhuman species, but not in our closest living relatives, the other great apes. The patchy distribution of proactive prosociality across species is suggestive of convergent evolution, raising the question whether the prevalence of proactive prosociality across primate species can be attributed to a particular socioecological factor. If this conjecture is confirmed, the same explanation could also account for the evolution of human proactive prosociality, and we would not need uniquely human evolutionary mechanisms, such as cultural evolution or gene-culture coevolution^{2,3} to explain its origins in our species.

Various hypotheses have been put forward to explain interspecific variation in proactive prosociality, including that it is contingent on high cognitive ability^{7,8}, high social tolerance⁹, the need to coordinate behaviour in the context of foraging^{1,10,11}, strong social bonds or allomaternal care^{7,12–14}. So far, however, it has been impossible to test these hypotheses because the available data lack comparability⁵, for three main reasons. First, in humans, sharing, helping and comforting follow distinct developmental trajectories¹⁵ and are regulated by different neural mechanisms¹⁶. Hence, these different mechanisms may have independent evolutionary histories. The various paradigms used to assess prosocial behaviour in nonhuman primate species may therefore have tested for different kinds of prosocial behaviour^{17,18}, such as for reactive prosociality in targeted helping tasks and proactive prosociality in dyadic provisioning games, in which individuals can opt to provide food to a partner at no or some small cost. Since the focus here is on proactive prosociality, only a subset of prosociality studies, covering a small number of species, would be available to test the various functional hypotheses. Second, it has become evident that prosociality studies are highly susceptible to seemingly trivial methodological differences⁶, even within a single paradigm. Recent reviews have shown that some widely used dyadic provisioning games to assess proactive prosociality can yield markedly different outcomes due to small differences in payoff distributions¹⁹ or payoff representations (for example, tokens versus real rewards^{7,20,21}). Third, studies differ with regard to whether dyads were preselected according to specific criteria, to make it more likely to detect prosocial behaviour in a species^{22,23}. While such procedures are valid in studies aiming at a proof-of-principle, they hamper quantitative comparisons across studies and thus across species. Thus, despite a large number of prosociality studies produced over the last years, it remains difficult to distinguish true species differences from differences that result from methodological heterogeneity of the respective studies^{5,6}.

To identify the evolutionary forces that may drive proactive prosociality, we first measured proactive prosociality in a large

number of species with a strictly standardized and previously validated experimental design²⁴. In this group service paradigm, individuals are tested in their social group and can provide fellow group members with food without obtaining any food for themselves. We applied this test to 24 social groups of 15 primate species, ranging from lemurs (two species) to New World monkeys (seven species), Old World monkeys (two species) and apes (four species, including *Homo sapiens*). In a second step, we examined correlated evolution between proactive prosociality and several socioecological factors hypothesized to contribute to variation in this trait. To disentangle the explanatory value of all the hypothesized factors, we used phylogenetic linear regressions models to control for phylogenetic non-independence of the species values, and an information-theoretic approach to model selection. To establish the general primate pattern, we initially analysed the impact of each of the potentially relevant factors in a data set that only contained nonhuman species. We then added the data on humans to test whether our species fits the general primate pattern.

According to the first hypothesis, proactive prosociality is cognitively demanding and thus constrained by cognitive abilities, in particular those related to Theory of Mind reasoning^{7,8}. As a proxy for cognitive ability, we included overall brain size in the analyses, as it is tightly linked to various measures of cognitive performance in nonhuman primates²⁵. Alternatively, proactive prosociality may be cognitively demanding because it requires inhibitory control to suppress the pre-potent tendency to consume the food oneself. The presence of fission–fusion dynamics in social organization has previously been identified as an important convergent factor for the evolution of inhibitory control²⁶, and was thus also included in our analyses.

Second, variation in proactive prosociality among primates may be linked to social tolerance. According to the self-domestication hypothesis⁹, prosocial behaviour arises as a correlated by-product of natural selection for increased tolerance and against aggression. We therefore also assessed social tolerance in each group and included it in our analyses.

Third, the need to coordinate behaviour in the context of foraging has been argued to drive proactive prosociality^{1,10,11}. Among nonhuman primates, the highest coordination in foraging activity occurs in cooperative hunting. We therefore also included the presence of cooperative hunting as an explanatory variable in our models.

Fourth, prosociality may be most prevalent among partners with strong social bonds. The strength of social bonds varies among primate species, and also whether they occur predominantly among males²⁷, among females²⁸ or in mated pairs. These strong bonds are typically accompanied by cooperation, which may produce species differences in proactive prosociality. We therefore included these various types of social bonds as factors in our analyses. Because within a species, prosociality may only be expressed within the respective bond classes, we also examined intraspecific patterns and analysed in the relevant species whether proactive prosociality was over-represented in male–male dyads, female–female dyads or pair mates.

Fifth, the cooperative breeding hypothesis predicts that proactive prosociality is linked to the amount of allomaternal care (care by non-mothers) provided to offspring^{7,12–14}. For cooperative breeding to work, caretakers must proactively seek opportunities to provide food or other forms of help¹². Indeed, within nonhuman primates, systematic proactive food sharing only occurs naturalistically in cooperatively breeding callitrichid monkeys, who also show the highest levels of allomaternal care¹⁸. We estimated the extent of allomaternal care through an updated version of a previously developed allocare score²⁹, which was

Table 1 Comparative tests of the hypotheses for the evolution of proactive prosociality.				
Hypothesis	Test variables	Delta AICc		
		Excl hum	Incl hum	
Cognitive ability	Brain size	19.9	29.3	
	Fission fusion as proxy for inhibitory control	23.8	29.4	
Social tolerance	Evenness of access to highly preferred and highly clumped food across group members (<i>J'</i>)	18.4	20.8	
Coordination of foraging activities	Presence of cooperative hunting within a species	23.6	29.4	
Strong social bonds*	Presence of male-male bonds within a species	23.8	29.4	
	Presence of female-female bonds within a species	20.5	24.3	
	Presence of pair bonds within a species	16	19.2	
	Extent of allomaternal care	0	0	
Allomaternal care				

AICc, Akaike Information Criterion corrected for small sample size; Excl hum, excluding humans; Incl hum, including humans.
Last two columns: fit of unifactorial PGLS models in explaining proactive prosociality in nonhuman primates, expressed as difference in AIC value from the best-fitting model, in the data set excluding and including *Homo sapiens*. In both data sets, the extent of allomaternal care best predicts proactive prosociality.
*The bonding hypotheses were also not supported by within-species analyses at the dyadic level. Thus, proactively prosocial provisioning was neither more likely within male-male dyads than within other dyad types in species with male bonding, nor within female-female dyads than within other dyad types in female-bonded species, nor between pair mates than within other dyad types in pair-bonded species.

highly correlated with various other ways of quantifying allomaternal care.

Our results demonstrate that the extent of allomaternal care provides the best explanation for the distribution of proactive prosociality among primate species, including humans. This conclusion is not affected when using different ways of quantifying allomaternal care. Importantly, we find no support for any of the other hypotheses, even when more refined analyses of within-species, dyad-level variation are conducted. The adoption of extensive allomaternal care by our hominin ancestors thus provides the most parsimonious explanation for the origin of human hyper-cooperation.

Results

Reliabilities. We assessed the inter-rater reliabilities by a rater who was not the experimenter of the respective group, for 10% of all of the 389 test sessions, which included 50% of all videos of test sessions 4 and 5 of phase IV, on which the main analyses were based. The reliabilities for the transfers ranged between Cohen’s Kappa = 0.89 and 1 per test session, with an average of 0.99 (s.d. = 0.03); the reliabilities for the reaching data ranged between 0.67 and 0.83 (average = 0.75, s.d. = 0.07). All analyses were based on the data from the first rater.

Between-species variation in proactive prosociality. In non-human primates, among the various potential factors (Supplementary Tables 1–3), allomaternal care emerged as the best predictor in unifactorial analyses of the interspecific variation in proactive prosociality (Table 1, Fig. 1), along with weakly significant effects of social tolerance and pair bonds (both positive) and brain size (negative; Fig. 2). Moreover, in all models containing a combination of any two of these factors, as well as their interactions, allomaternal care emerged as the only significant effect on proactive prosociality, whereas none of the interaction effects were significant (Supplementary Table 4). The best-fitting model, chosen according to the lowest value of the Akaike Information Criterion corrected for small sample size, included allomaternal care only (Fig. 1, Table 1).

In the next step, we repeated the same analyses after adding the results from the human subjects (three groups of 4:5–7:1-year-old Kindergarten children) into the nonhuman primate data set. As in the previous data set, the best model only included allomaternal care. Unifactorial effects were again present for social tolerance and pair bonds, but lost most of their explanatory power in two-factorial models that also included allomaternal care (Supplementary Table 5).

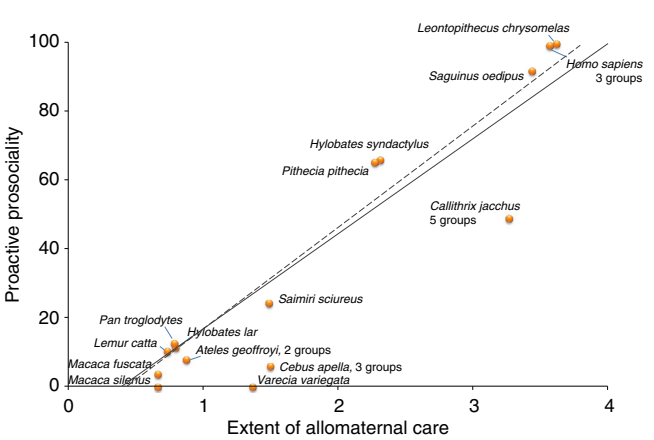


Figure 1 | Proactive prosociality as a function of the extent of allomaternal care in a sample of 15 primate species. Solid regression line: excluding *Homo sapiens*; dotted regression line: including *Homo sapiens*. Proactive prosociality refers to the percentage of trials with food transfers to other group members during the last two test sessions in phase IV of the experiment, by individuals passing control criterion 1.

To assess how well the human data fit the general primate pattern, we also calculated the standardized residuals for all species (mean = 0, s.d. = 1), including humans, relative to the regression line based on nonhuman primates only. Humans deviated from this regression line by less than one s.d. (0.85), indicating that they do not represent an outlier and therefore follow the general primate pattern. Thus, allomaternal care provides the best explanation for the distribution of proactive prosociality among primate species, including humans. Importantly, these results are robust to different ways of quantifying allomaternal care (Supplementary Table 6).

Dyad-level variation in proactive prosociality. Because some of these alternative hypotheses also make predictions regarding variation within the groups, more refined tests of dyad-level patterns are also possible. First, if proactive prosociality is linked to male bonding, we expect more transfers between male-male dyads in male-bonded species (spider monkeys: *Ateles geoffroyi*; chimpanzees: *Pan troglodytes*) than between other types of dyads. However, in test sessions 4 and 5 of phase IV, in both species transfers between male-male dyads did not occur more than expected (Fig. 3; chimpanzees: $\chi^2 = 2.48$, df = 1, ns; spider monkeys: absolute number of transfers too low to allow for

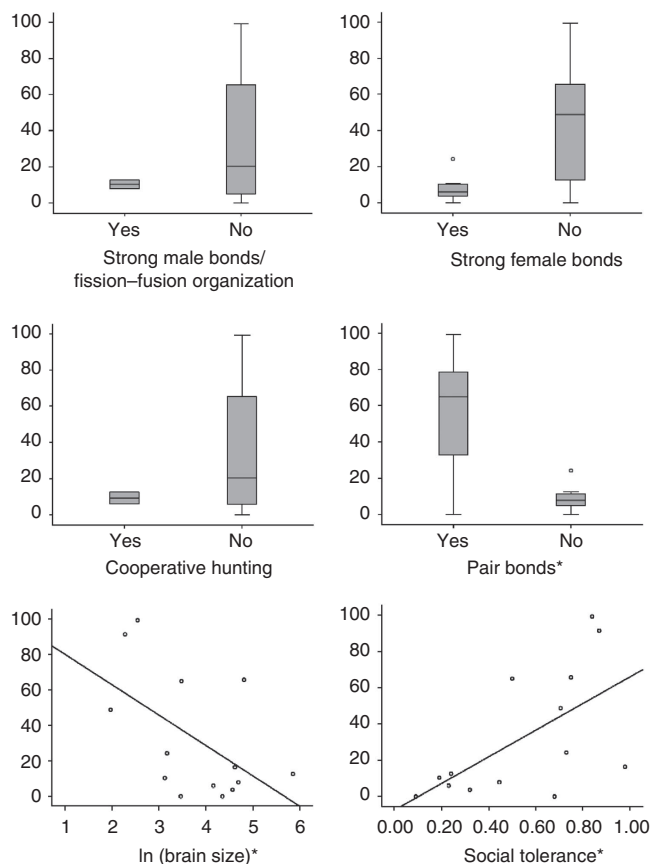


Figure 2 | Proactive prosociality as a function of the explanatory variables other than the extent of allomaternal care (without *Homo sapiens*). The presence ($n = 2$) or absence ($n = 12$) of strong male bonds or fission-fusion organization in a species, of strong female bonds (present in five species, absent in nine), of cooperative hunting (present in two species, absent in 12), of pair bonds (present in seven species, absent in seven) as well as brain size and social tolerance. The box plots represent medians (black horizontal lines), inter-quartile range (grey boxes), minima and maxima (whiskers) as well as outliers (dots) * $P < 0.05$.

statistical testing), and the pattern of within-group variation is thus consistent with the rejection of the male bonding hypothesis.

Second, the same prediction of a male bias in transfers results from the cooperative hunting hypothesis, because group hunting is predominantly biased towards males, both in chimpanzees and capuchin monkeys²⁷. However, in both species, transfers are not biased towards male-male dyads (Fig. 3: capuchin monkeys: absolute number of transfers too low to allow for statistical testing), which is inconsistent with the cooperative hunting hypothesis.

Third, if female bonding determined the variation in proactive prosociality, we would expect a bias towards female-female dyads among the female-bonded species (macaques: *Macaca fuscata*, *Macaca silenus*; squirrel monkeys: *Saimiri sciureus*; ring-tailed lemurs: *Lemur catta*; capuchin monkeys: *Cebus apella*). Overall, transfers were rare in these species and did not allow for statistical testing; nevertheless, the transfers that did happen were not biased towards female-female dyads (Fig. 3 for squirrel monkeys, capuchin monkeys and ring-tailed lemurs). In *Macaca silenus*, no transfers occurred in sessions 4 and 5; in *Macaca fuscata*, only seven transfers occurred, and in six of these, the juvenile daughter of the dominant female was involved. Taken together, the within-group variation in female-bonded species thus confirms the rejection of the female bonding hypothesis.

Finally, if pair bonding were an important independent determinant of proactive prosociality, we would expect most transfers to occur between pair mates. Although pulling was non-random between dyad types in the sakis (*Pithecia pithecia*: $\chi^2 = 15.6$, $df = 1$, $P < 0.001$), the male never pulled for anybody and transfers between the pair mates were absent. In the gibbons (*Hylobates lar*), we could not test this prediction because the breeding pair could only pull for each other (the infant was too young to pull or take food). In the siamang (*Hylobates syndactylus*) group, composed of the breeding pair and a juvenile son, transfers were not more likely between the pair mates ($\chi^2 = 0$, $df = 1$, nonsignificant) and all transfers were initiated either by the father (33.3%) or the son (66.6%). In the ruffed lemurs (*Varecia variegata*), no transfers occurred in test session 4 and 5. In common marmosets, transfers were also not biased towards the breeding pair but instead occurred less than expected by chance ($\chi^2 = 8.5$, $df = 1$, $P = 0.004$). In cotton-top tamarins (*Saguinus oedipus*), the breeding female had died, so no test was possible. Overall, then, no bias towards more transfers within the pair bond was apparent.

The only exception was encountered in the lion tamarins (*Leontopithecus chrysomelas*), where transfers were more likely between breeders than between other dyads ($\chi^2 = 81.27$, $df = 1$, $P < 0.001$). However, in this group, 37.5% of the food rewards made available through pulling within the breeding pair were further shared with an infant, and food sharing was presumably constrained by increasing satiation of the immature over the 70 test trials, rather than by a lack of willingness to share. This pattern does not support the idea that pair mates exclusively pulled for each other. Furthermore, when we removed the breeding female from the group for an additional test session with the remaining group members, this did not appreciably decrease the overall number of transfers compared to the last regular test session (98.6% in the last regular test session, compared to 90.0% in the additional test session without the breeding female). Taken together, these within-group findings do not support pair bonding as the sole determinant of proactive prosociality.

The within-species, dyad-level analyses therefore likewise did not provide support for any of the bonding hypotheses, corroborating the result of the species-level analyses.

Discussion

The results of the between-species comparative analyses suggest that allomaternal care best predicts proactive prosociality in primates. This finding is corroborated by the results of the within-species tests of dyadic patterns (see Supplementary Discussions for details) and unlikely to be based on a methodological artefact (see Supplementary Methods for details).

While the group service paradigm deployed here is simple and robust, it has two limitations as compared with the usual tests involving separated dyads. First, its statistical power is limited, because groups (or even species) rather than individuals represent independent data points. However, group testing ensures greater ecological validity than dyadic tests because it assesses the behaviour of individuals in their naturalistic context, rather than after separation from the rest of the group; ecological validity is crucial to testing functional hypotheses. A second weakness, which it shares with other prosociality tests, is that it may be sensitive to minor methodological changes (for example, size of the apparatus or time of testing relative to last feeding). However, these factors do not systematically covary with species in the present data set. In fact, we explicitly controlled for such potential effects by standardizing the methods across groups and species through the use of identical protocols and experimental setups. Whether changes in the protocol or experimental setup indeed

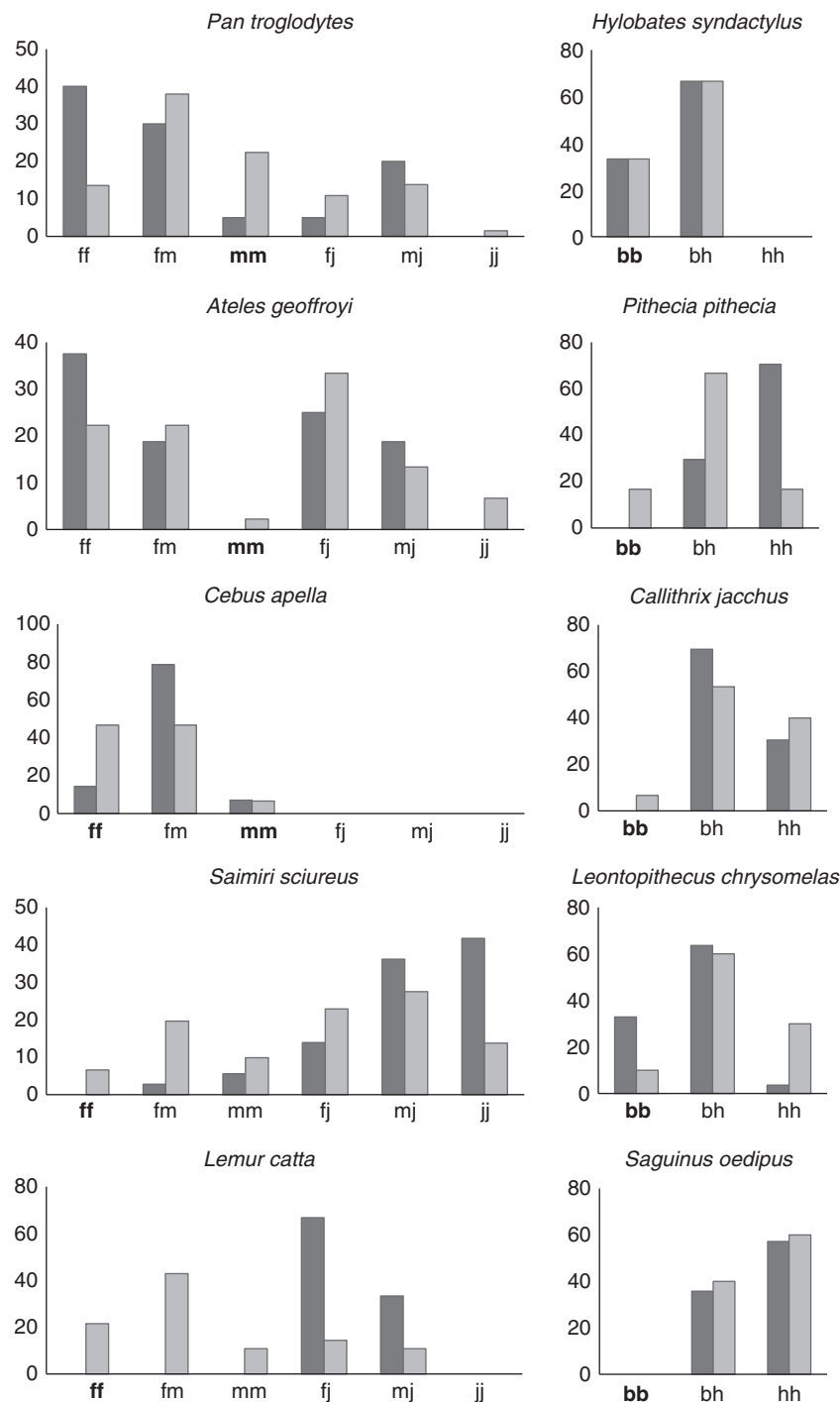


Figure 3 | Distribution of transfers per dyad type. Dyad types printed in bold are expected to be over-represented by different alternative hypotheses, that is, in male-male dyads (mm) in species with strong male bonding and/or cooperative hunting, in female-female dyads in species with strong female bonding or in mate pairs in pair-bonded species. X axis: dyad type, y axis: % of transfers in sessions 4 and 5 of phase IV. Light-grey bars represent expected values, dark-grey bars observed values. b, breeder; f, adult female; j, juvenile; h, offspring of breeding pair, that is, helpers; m, adult male. *Pan troglodytes*: 55 female-female dyads (55ff), 154fm, 91mm, 44fj, 56mj, 6jj; *Ateles geoffroyi*: 10ff, 10fm, 1mm, 15fj, 6mj, 3jj; *Cebus apella*: 21ff, 21fm, 3mm; *Saimiri sciureus*: 10ff, 30fm, 15mm, 20fj, 24mj, 6jj; *Lemur catta*: 1ff, 6fm, 3mm, 6fj, 9mj; *Hylobates syndactylus*: 1bb, 2bh; *Pithecia pithecia*: 1bb, 4bh, 1hh; *Callithrix jacchus* (Jojoba): 1bb, 8bh, 6hh; *Leontopithecus chrysomelas*: 1bb, 6bh, 3hh; *Saguinus oedipus*: 0bb, 4bh, 6hh).

influence performance in the group service paradigm, and in what way, remains to be established in future studies.

A more general limitation of our approach is that we used only a single test for the proactively prosocial motivation, whereas convergent results of multiple tests would enhance confidence in our findings. Thus, the development of a robust standardized

dyadic test, and its systematic application to multiple species, to complement the group service approach, continues to have a high priority. Such dyadic tests would also provide an important complement to the tests of within-group patterns of proactive prosociality across species applied in the group service paradigm.

Table 2 | Origin and composition of the social groups tested with group service.

Species	Origin	Group composition
Prosimians		
<i>Lemur catta</i> (ring-tailed lemur)*	German Primate Center, Göttingen, Germany	2f, 3m, 3j
<i>Varecia variegata</i> (ruffed lemur)*		1f, 4m, 1j
New world monkeys		
<i>Ateles geoffroyi</i> (spider monkey)*	Animaya Zoo, Merida, Mexico	5f, 3m, 5j
<i>Ateles geoffroyi</i>	Zoo Basel, Basel, Switzerland	5f, 2m, 3j
<i>Pithecia pithecia</i> (saki)		3f, 1m, 1i
<i>Saimiri sciureus</i> (squirrel monkey)	Zoo Rapperswil, Switzerland	5f, 6m, 4j, 4i
<i>Callithrix jacchus</i> (common marmoset)–Kaliung†	Primate station of the Anthropological Institute and Museum, Zürich, Switzerland	2f, 5m
<i>Callithrix jacchus</i> –Jojoba		3f, 3m
<i>Callithrix jacchus</i> –Vreni†		5f, 2m
<i>Callithrix jacchus</i> –Juno		4f, 2m
<i>Callithrix jacchus</i> –Mina		2f, 2m
<i>Saguinus oedipus</i> (cotton-top tamarin)	Primate station of the Anthropological Institute and Museum, Zürich, Switzerland	2f, 3m
<i>Leontopithecus chrysomelas</i> (lion tamarin)		2f, 3m, 1i
<i>Cebus apella</i> (capuchin monkey)*	CNR Primate Centre, Institute of Cognitive Sciences and Technologies, Rome, Italy	3f, 3m
<i>Cebus apella</i> *		7f, 3m, 1i
<i>Cebus apella</i>	Zoo al Maglio, Magliaso, Switzerland	2f, 2m, 3j, 1i
Old world monkeys		
<i>Macaca fuscata</i> (Japanese macaque)	Zoo Parc Overloon, Overloon, Netherlands	5f, 2m, 3j, 1i
<i>Macaca silenus</i> (lion-tailed macaque)		4f, 1m, 1j
Apes		
<i>Hylobates syndactylus</i> (siamang)*	Landestiergarten Herberstein, Stubenberg, Austria	1f, 1m, 1j
<i>Hylobates lar</i> (gibbon)	Tiergarten Schwaigern, Leintal, Germany	1f, 1m, 1i
<i>Pan troglodytes</i> (chimpanzee)*		11f, 14m, 4j
<i>Homo sapiens</i> (humans), 4:8–5:9 years	Kindergärten der Stadt Zürich, Switzerland	4f, 1m
<i>Homo sapiens</i> , 4:5–5:2 years		5f, 3m
<i>Homo sapiens</i> , 6:3–7:1 years		3f, 5m

f, female; i, infant; j, juvenile; m, male.

*Indicate groups with experimental experience before the group service test.

†Groups with experience with prosociality tasks.

f, female; i, infant; j, juvenile; m, male.

*Indicate groups with experimental experience before the group service test.

†Groups with experience with prosociality tasks.

Nonetheless, the various controls applied in the present study indicate that it is unlikely that any artefact or systematic bias is responsible for the strong pattern obtained here. For a more thorough discussion of how the present results link to earlier prosociality studies, see Supplementary Discussion.

Having established that the result obtained here is likely to survive additional testing, we can now address its implications. Unlike any of the other apes, humans have become cooperative breeders, perhaps in response to moving into savannah habitats, where immature foraging success was severely impaired^{14,30}. The pattern reported here therefore supports an evolutionary scenario in which the adoption of shared childcare by our ancestors modified our prosociality, by convergently adding a proactive motivation, as is the rule in other primate lineages that adopt cooperative breeding. This motivation may have transformed the individualistic cognitive skills as present in great apes (but not in monkeys) into the human-typical shared intentionality¹, which in turn produced cascading cognitive effects via language, collaboration and instructed learning¹⁰.

These results therefore support the cooperative breeding hypothesis^{12–14} for the evolution of this critical element of human hyper-cooperation. A major feature of this hypothesis is that it explains why only our hominin ancestors, and none of the other, independently breeding great apes, took this extraordinary evolutionary trajectory¹⁴. This hypothesis can also explain why our hyper-cooperation also extends to non-kin. First, obligate

cooperative breeders usually contain mostly kin, that is, offspring of the unrelated breeding pair, but when unrelated individuals join these groups, their behaviour is often indistinguishable from that of the related helpers^{22,31,32}. Second, human forager groups contain multiple mated pairs, and obligations towards the mate's relatives, which genetically speaking are non-relatives, are also important. Thus, once established in our ancestors, the proactively prosocial psychology may have become generalized toward all in-group members³³.

Finally, this general biological explanation for the origin of human hyper-cooperation also helps delineating the contexts in which uniquely human evolutionary processes relying on cultural evolution, group selection, cultural group selection or gene-culture coevolution^{1–3} are needed to bring about human hyper-cooperation. Since in small face-to-face groups, hyper-cooperation works well without additional mechanisms such as altruistic punishment^{2,3}, it is likely that these processes only became necessary to maintain hyper-cooperation in large, anonymous societies, but were not needed earlier.

Methods

Subjects. Table 2 provides an overview of the subjects that participated in the experiment. In various institutions, we tested all subjects in their social group, in their home cage in between the regular feedings. The animals were neither food- nor water-deprived. As rewards, we used special treats that were highly preferred by all group members, as established before the test. Immatures too small to handle the apparatus or take food through the wire mesh were omitted in measures of

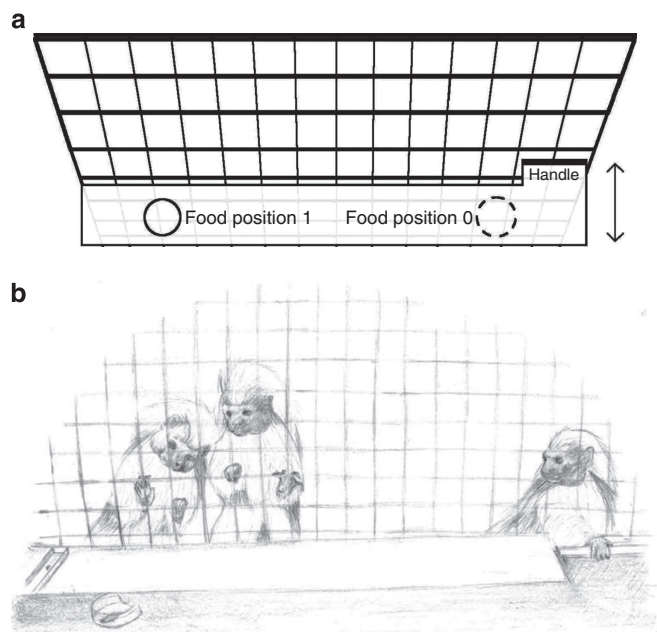


Figure 4 | Group service apparatus. (a) Schematic drawing. The board with the food bowl in position 0 or 1 is attached outside the wire mesh of the home cage. Subjects can pull the handle to move the board to within reach (as indicated by the grey arrow), but the board slides back if the subject releases the handle. Subjects can pull the board and retrieve the food themselves if the food bowl in position 0 is baited. However, food baited in position 1 can only be made available if one individual pulls the handle and holds the board within reach, while a second individual retrieves the food. (b) A cotton-top tamarin (*Saguinus oedipus*) pulls the board to provide food in the transparent bowl to other group members. Line drawing after still frame.

social tolerance and whenever the analysis involved calculation of expected values. Other individuals who had not reached sexual maturity at the beginning of the test were included and classified as juveniles.

The human children were tested in their Kindergarten groups, in a separate room but in the same building as their classroom. To minimize the possibility that socially desired behaviour would be elicited by the presence of an authority figure, we tested human children in the absence of teachers (see also Supplementary Methods for further details on testing human children, and Supplementary Fig. 1). The experiments with the nonhuman primates had been approved by the relevant authorities; those in Zurich and Basel by the Kantonales Veterinäramt, under the license numbers 4389 and 2541, respectively. For the human children, the parents gave written informed consent for their children's participation, and the study was approved by the Ethik-Kommission of the Kinderspital Zurich, Unterkommission SPUK.

The group service paradigm. We used an approach explicitly developed to provide a standardized measure of both proactive prosociality and social tolerance, the group service paradigm²⁴. In essence, social groups are presented with food that is out of reach, on a board outside their home cage (Fig. 4). By pulling the handle of the board, an individual can pull food within reach of other group members. However, the pulling individual can never obtain the food for itself, because (i) the food is too far away from the handle to both pull and simultaneously retrieve the food and (ii) the board slides back automatically as soon as the handle is released. The only way for any group member to obtain food is when some other individual pulls the handle and holds it long enough for the group member to retrieve the food from the board. The group service experiment consists of five phases, and subjects have to pass predefined criteria to enter the subsequent phases. Various control conditions and criteria are an integral part of the group service approach to ensure that the behaviour indeed qualifies as proactive prosociality²⁴.

The group service paradigm provides comparable data due to the standardization of the experimental procedure, but also has additional advantages. First, the setup is cognitively non-demanding, and even small-brained primate species, like callitrichid monkeys, can demonstrably understand it and pass all necessary control conditions²⁴. Second, the test does not require that individuals be separated from their group mates, which may especially affect performance in highly interdependent species. Third, the test quantitatively assesses the degree of proactive prosociality as it occurs in a naturalistic situation, rather than in specific dyads or under specific circumstances. Fourth, phase II of the group service

paradigm also provides a repeatable measure of social tolerance in the group concerned.

Apparatus and procedure. The apparatus consisted of a board placed outside the wire mesh of the home cage. A food bowl could be placed on top of the board (Fig. 4). If it was placed in position 0, a subject could pull the handle with one hand and access the food with the other hand. However, if the bowl was placed in position 1, which was always located more than two arms' lengths away from position 0, the subject pulling the handle was no longer able to access the bowl by herself. Position 0 was used in training and motivation trials, position 1 in test trials. Importantly, the board was mounted on inclined rails that ran perpendicular to the mesh, so that the board would slide down away from the cage unless it was pulled by the handle. Only if it was pulled by one individual and held in place close to the wire mesh would its content become accessible to the remaining subjects in the home cage. Successful food provisioning in the group service test thus required that one individual left the position closest to the food, moved to the position in front of the handle and pulled and held it in a way that was sufficiently coordinated to allow a second individual to retrieve the food.

The group service test was composed of five distinct experimental phases, and subjects had to pass predefined criteria to enter the subsequent phase.

Phase I, Habituation. The aim of phase I was to habituate the subjects to the apparatus, the basic procedure and the experimenter. The board with the food bowl in position 0 was fixed close to the wire mesh so that subjects could freely access the bowl without having to pull the apparatus. Pieces of favourite foods (minimum 10 pieces per subject) were provided sequentially in position 0 during 5 days, or until every subject had taken at least three pieces. In each trial, a piece of food was held up by the experimenter who drew the subjects' attention to it verbally by saying: 'look here!' This attention-getting procedure assured that all subjects of a group would pay attention to the setting, independent of cage size, and was used in all phases of the experiment. If necessary, dominant individuals were distracted from the apparatus by a second experimenter to make sure that all individuals would approach the apparatus.

Phase II, Social tolerance. In phase II, we quantified social tolerance in the feeding context, by placing 35 pieces of favourite food, one at a time, on the apparatus fixed within reaching distance of the subjects, as in phase I. When a piece of food was taken by an individual, we waited until the food was completely consumed before starting the next trial by saying 'look here!' and placing the next piece of food in the bowl. We recorded the percentage of food items received by each group member and calculated the evenness J' of this distribution³⁴, as a measure of how equitable food was obtained by group members, and thus, how good the odds of subordinates were of having access to the food. When food was shared (passively or actively), it was counted as food received by both group members involved, independently of the amount of food eaten by each individual. To assess the repeatability of this measure of social tolerance, we conducted this test twice, on two consecutive days. Across the 24 primate groups, the evenness of the distribution on day one was strongly correlated with that on day two ($r^2 = 0.722$, $P < 0.001$), which provides evidence for high repeatability of this measure of social tolerance. For the main analyses, we calculated the amount of social tolerance of each group based on the combined data of both days.

Phase III, Training. In phase III, the subjects learned to pull the handle and hold it to retrieve the food. The board was now in its original position, at some distance from the wire mesh, such that only the handle could be reached. Criterion was reached when the subjects were able to pull the handle, hold it with one hand and take food with the second hand, with the food bowl placed within one arm's length from the handle (Fig. 4, position 0). Pieces of food were provided until each subject passed the criterion of pulling the food within reach for itself in at least seven trials (again, if necessary after distracting dominant individuals). For individuals who had difficulties in learning the task, we added intermediate steps, such as placing the food on top of the handle, directly in front of the handle, near the handle with increasing distances to it and finally in the food bowl. Passing the criterion of phase III corresponds to passing the knowledge probe that individuals did understand how the apparatus worked.

Phase IV, Group service. In phase IV, the core of the group service experiment, we measured proactive prosociality. The board was in its original position as in phase III, but food was now placed in position 1, too far away for an individual to pull the board and at the same time retrieve the food for itself. Essentially, we assessed how much food each group was able to make available to its members, which required individuals to forgo the reward for themselves and instead move away from the food to pull and hold the handle and provide the food to its group mates.

In phase IV, we alternately ran five test sessions and five control sessions. Each session consisted of 70 regular and 14 motivation trials. During regular trials, food was placed in position 1 and could only become available to the group if an individual would forgo the reward and instead pull for its group members. During motivation trials, food was placed in position 0 and could be obtained by individual effort (like in phase III). Motivation trials were inserted after every 5th regular trial, resulting in a total of 84 trials, including the very first trial, which was also a motivation trial. Motivation trials, which included the vocal attention getters, were included to assess whether the animals were interested in the reward until the end of each test, and would continue to attend to the experimental setup. If no one

would take the food in more than two consecutive motivation trials in less than 1 min, the experimenter ended the session. In the majority of groups, all motivation trials were always taken, both in test and control sessions (exceptions where food was not taken in two consecutive motivation trials at least once over the five test and five control sessions: siamangs, one group of spider monkeys, lemurs and kattas).

During test sessions, the food bowl was baited at the beginning of each trial by holding up the food item, attracting the group's attention by a vocal attention getter ('look here!') and conspicuously placing the food item in the bowl. The trial ended either when the food had been provided to a group member or after 1 min had elapsed. If no food was taken in a trial, the experimenter started the next trial by holding up the food item from the bowl again, showing it demonstratively to the group, attracting their attention vocally and placing it back in the food bowl.

During control sessions, the food bowls were not baited with food in regular trials. Instead, the experimenter held up a small stick, touched the bowl with it audibly and simultaneously used the same verbal attention getter as during the experimental trials. This control served to exclude the possibility that pulling occurred simply to explore the apparatus itself, or as mere play behaviour. As in the test sessions, motivation trials, in which real food was provided, were inserted after every 5th regular trial.

Proactive prosociality was calculated as the corrected percentage of food provisioning in the last two test sessions for each group. The last two test sessions were chosen because by then, all subjects had had ample opportunity to learn that they could not get the food by themselves by pulling the apparatus, which in the very first trials may have led to false positives. The last two test sessions thus yield the most conservative estimate of proactive prosociality, but the results do not change if we take the total percentage of food provisioning overall test sessions. Furthermore, the percentage was corrected by including in this measure only provisioning by individuals who passed the criterion of pulling significantly more in test versus control sessions, but note that both measures are highly correlated (Supplementary Fig. 2).

Phase V, excluding alternative explanations for sustained provisioning—If sustained provisioning occurred over the five test sessions in phase IV, it could still be that transfers occurred by mistake because the pulling subjects had not understood that they wouldn't be able to obtain the food themselves, and had not learnt this during the five test sessions. Even though the animals would have had numerous opportunities to learn that pulling food in position 1 was never rewarded, it could be argued, especially for smaller-brained species such as callitrichids that 350 trials are not sufficient to learn so. In the final phase V, we therefore tested this understanding, but obviously could only do so in those groups that had shown sustained provisioning in phase IV, that is, who continued to provide food to partners at stable rates throughout the 5 test sessions of phase IV.

Phase V was identical to phase IV, except that physical access to the food bowl was now blocked by a fine-meshed grid attached to the home cage in front of position 1, leaving visual and olfactory cues present. Thus, even if the tray was pulled to within reach, no one could ever obtain the food. In the sakis and in one group of common marmosets, instead of blocking the access with a fine-meshed grid, we moved the apparatus to the edge of the cage so that the outer part of the apparatus would overhang the length of the home cage. Thus, the apparatus could still be pulled but the food would nevertheless not become available to the other group members.

We again ran five test sessions (position 1 baited) and five control sessions (position 1 empty) with the grid always in place, on alternating days. Each session consisted of 70 trials and additional motivation trials interspersed after every 5th regular trial (during motivation trials, food was again available and accessible in position 0). If in phase IV, pulling the baited tray in position 1 occurred for any reason other than intentionally providing food (for example, a persistent inability to inhibit pulling the baited tray due to the salient visual and olfactory cues), pulling should continue in phase V at the same level as during phase IV. However, if pulling in phase IV occurred to provide food to group members, pulling in phase V should decrease over time more consistently than in phase IV because pulling in phase V did not result in providing food to group members.

Data coding and reliabilities. All sessions in phase III, IV and V were video recorded. During the experiments, data were also collected by hand, including whether an individual pulled or not within a given trial, whether a transfer occurred and if so, the identity of the donor and the recipient. This data was later verified with the video clips by the experimenter. In case of inconsistencies, the true values based on the video clips were used. Reaching was only coded from the videos after the experiment, for test session 5 of phase IV. For each regular trial, we coded whether an individual tried to reach for the food in position 1 by extending its arm (or tail in the case of spider monkeys) outside of the wire mesh in the direction of the food reward. However, we only included reaching attempts that could be perceived by a second individual that was close enough to reach the apparatus with one leap (exact distances differed according to the respective species).

Validity of the group service approach. The group service paradigm requires several criteria to be fulfilled to conclude that food deliveries are due to proactive prosociality²⁴ (see Supplementary Methods for details). First, subjects must understand the task. They must pass various knowledge probes and control

conditions to proceed to the experiment (Supplementary Table 7). In particular, the results must not reflect the absence of sufficient inhibitory control. Ideally, an alternative measure that controls for inhibitory control (that is, difference scores for which pulling rates during control sessions are subtracted from pulling during test sessions, Supplementary Table 8) produces the same results as those obtained with the absolute measure used for the main analyses. Second, species with high rates of proactively prosocial pulling must maintain high rates throughout all five test sessions, and not decline over time, as would be expected if animals unintentionally provisioned others in the beginning and gradually learned they were doing so (Supplementary Fig. 3). Third, we must exclude that reactive prosociality drives the results, that is, that begging is not necessary and other signs of need by recipients ineffective (Supplementary Fig. 4). Fourth, phase V is added to further demonstrate the understanding of the consequences of their pulling. However, this is only necessary for those groups passing the three criteria mentioned above and continuing to provide food in more than 40% of all trials in the last test session. Note that for the human children, phase V was modified (Supplementary Methods and Supplementary Fig. 6).

Finally, one could argue that rather than testing different groups, we only assess the behaviour of the most dominant individual per group because this is the only individual in the group enjoying near-complete freedom in behaviour. To test this possibility, we assessed whether the relationship between the extent of allomaternal care and proactive prosociality also holds at the group level (GLM; response: proactive prosociality, random effect: species. Note that phylogenetic structure can only be taken into account in species-level analyses. However, lambda was low or 0 in most of the species-level analyses performed in the main analyses, suggesting that phylogenetic structure has only a marginal effect in the present data set). Confirming our main conclusion, the relationship between allomaternal care and proactive prosociality is also stable when we test at the group level ($F_{(13,10)} = 6.24$, $P = 0.003$, Supplementary Fig. 5).

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Author contributions

J.M.B. and C.P.v.S. designed research; J.M.B., O.A., C.Fin., C.Fic., A.H., J.H., Z.K.K., E.J.M., E.M., R.R., K.R., B.S. and S.W. performed research; J.M.B., K.I. and C.P.v.S. analysed data; J.M.B. and C.P.v.S. wrote the paper. All authors discussed the results and commented on the manuscript.

Additional information

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RESEARCH ARTICLE

Why Do Orangutans Leave the Trees? Terrestrial Behavior Among Wild Bornean Orangutans (*Pongo pygmaeus wurmbii*) at Tuanan, Central Kalimantan

ALISON M. ASHBURY¹, MARY ROSE C. POSA², LYNDY P. DUNKEL¹, BRIGITTE SPILLMANN¹, S. SUCI UTAMI ATMOKO³, CAREL P. VAN SCHAIK¹, AND MARIA A. VAN NOORDWIJK^{1*}

¹Anthropological Institute and Museum, University of Zurich, Zurich, Switzerland

²Department of Biological Sciences, National University of Singapore, Singapore

³Fakultas Biologi, Universitas Nasional, Jakarta, Indonesia

Orangutans (genus *Pongo*) are the largest arboreal mammals, but Bornean orangutans (*P. pygmaeus* spp.) also spend time on the ground. Here, we investigate ground use among orangutans using 32,000 hr of direct focal animal observations from a well-habituated wild population of Bornean orangutans (*P. p. wurmbii*) living in a closed-canopy swamp forest at Tuanan, Central Kalimantan, Indonesia. Ground use did not change with increasing observation time of well-habituated individuals, suggesting it was not an artifact of observer presence. Flanged males spent the most time on the ground (ca. 5% of active time), weaned immatures the least (around 1%). Females and immatures descended mainly to feed, especially on termites, whereas flanged males traveled more while on the ground. Flanged males may travel more inconspicuously, and perhaps also faster, when moving on the ground. In addition, orangutans engaged in ground-specific behavior, including drinking from and bathing in swamp pools. Supplementary records from 20 ground-level camera traps, totaling 3986 trap days, confirmed the observed age-sex biases in ground use at Tuanan. We conclude that ground use is a natural part of the Bornean orangutan behavioral repertoire, however it remains unclear to what extent food scarcity and canopy structure explain population differences in ground use. *Am. J. Primatol.* © 2015 Wiley Periodicals, Inc.

Key words: Borneo; orangutan terrestriality; *Pongo pygmaeus wurmbii*; ground travel; direct observation; camera trapping

INTRODUCTION

Orangutans (genus *Pongo*) are the only great apes found outside of Africa and are the largest habitually arboreal mammals. There are two recognized species of orangutans, *P. abelii* in Sumatra and *P. pygmaeus* in Borneo [Brandon-Jones, 2004; Nater et al., 2011]. Both orangutan species have very slow life histories, with late ages at first reproduction and extremely long interbirth intervals [Galdikas and Wood, 1990; Wich et al., 2004; Knott et al., 2009]. Their arboreality contributes to their low extrinsic mortality by keeping them out of reach of most natural predators [Jones, 2011; van Schaik & Isler, 2012]. Indeed, orangutans in Borneo—where tigers (*Panthera tigris*) have been extinct for millennia—are known to occasionally come down to the ground in natural forests [Wallace, 1869]. In contrast, terrestrial behavior among Sumatran orangutans—where the range of extant tigers overlaps almost the entire range of orangutans [Chundawat et al., 2011; Singleton et al., 2008]—has hardly ever been observed [Thorpe and Crompton, 2009]. Other possible selective pressures to maintain an

arboreal lifestyle include a relatively lower exposure to (intestinal) parasites and other pathogens by being away from the ground, and more recently, a lower risk of exposure to human activity [Ancrenaz et al., 2014; Woodford et al., 2002].

Many behavioral studies have noted terrestrial activity among orangutans [e.g. MacKinnon, 1974]. In the Bornean studies, the large-bodied flanged

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*Correspondence to: Maria A. van Noordwijk, Anthropological Institute and Museum, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland. E-mail: vnoord@aim.uzh.ch

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males are reported to travel more frequently on the ground than females or smaller unflanged males [Galdikas, 1979; Rodman, 1979; Thorpe & Crompton, 2009], whereas Sumatran flanged males do not use the ground [Thorpe & Crompton, 2006], except in emergencies, such as when fleeing from an opponent [Cant, 1987; van Schaik, 2004]. Travelling terrestrially may be beneficial for several reasons, including a reduced risk of falling if a supporting tree or branch breaks [Kehoe & Chan, 1986; Kraft et al., 2014]. Terrestrial travel is also thought to be energetically cheaper than arboreal travel, even for an ape anatomically adapted to arboreal travel [Cant, 1987; Begun & Kivell, 2011; Loken et al., 2013], and because the cost of climbing is directly proportional to body size [Thorpe et al., 2007], this would explain the observed ground-use bias towards the large flanged males. This economical travel option may allow flanged males to offset certain costs associated with their secondary sexual characteristics (for instance, their inability to keep up with fleeing females), and thus diminish the advantages of the unflanged stage [van Schaik et al., 2009; Dunkel et al., 2013]. Therefore, the Borneo–Sumatra contrast in predation pressure and degree of terrestriality may have affected inter-island differences in social organization and patterns of male developmental arrest.

This argument assumes that the animals' behavior is not influenced by the presence of human observers. Thus, an observed orangutan may use the ground less in the presence of an observer because the observer is perceived as a threat [Loken et al., 2013], or alternatively over time may come to use the ground more in the presence of an observer because their presence is perceived as an indication that the ground is safe [Grundmann, 2006; Russon et al., 2009].

Three recent studies have sought to investigate and quantify orangutan terrestrial behavior using indirect observation through ground-level camera traps. Loken et al. [2013], Ancrenaz et al. [2014], and Loken et al. [2015] reported frequent detection by camera traps of Bornean orangutans on the ground at several sites, including varying types of forest subjected to varying degrees of human disturbance. These camera-trap studies have convincingly shown that in the absence of human observers, (flanged) males use the ground rather frequently. However, the other age-sex classes were also recorded to be on the ground, albeit less frequently in most [Ancrenaz et al., 2014; Loken et al., 2015], but not all sites [Loken et al., 2013].

The frequency of ground use found in these camera-trap studies has led to much speculation about the proximate reasons why wild orangutans descend to the ground. If the forest structure allows, orangutans are capable of crossing considerable gaps in the canopy by tree swaying, which is often energetically less costly than descending to the

ground and climbing up again [Thorpe et al., 2007; Manduelli et al., 2011]. Thus, terrestriality for the sole purpose of crossing canopy gaps should rarely be efficient. Nevertheless, some recent studies have emphasized terrestriality especially to cross gaps in the forest [Ancrenaz et al., 2014; Rijksen & Meijaard, 1999] and have even suggested that once individuals are used to using the ground to cross canopy gaps, this would enable them to disperse across open terrain in fragmented habitat [Ancrenaz et al., 2014]. Alternatively, orangutans' ground use is not forced by canopy gaps, but used to travel over longer distances in continuous forest [Galdikas, 1979; Rodman, 1979] or to acquire terrestrial (fallback) food, water, or minerals [Cant, 1987; MacKinnon, 1974; Matsubayashi et al., 2011].

To identify the major causes of terrestriality, we present direct observational and camera-trap data of ground use (defined as any time during which an orangutan is in contact with the ground) among Bornean orangutans (*Pongo pygmaeus wurmbii*) of a mostly habituated natural population, inhabiting a peat-swamp forest without major canopy gaps. We first investigated whether the behavioral data show a strong bias due to habituation or observation difficulties. Then we examined the behavioral, environmental and spatial correlates of ground use. Finally, we summarize the evidence of orangutan ground use from camera traps in our study area.

METHODS

Study Site

Behavioral data were collected from July 2003–2010 on the natural population of Bornean orangutans in the Tuanan Orangutan Research Area, Mawas Reserve, Kalimantan Tengah, Indonesia (2° 09' S; 114° 26' E). The entire study area (approx. 7.5 km²) is homogenous peat-swamp forest, which has previously been subjected to selective logging, but had had (as of 2003) at least 5 years to recover [van Schaik et al., 2005]. There is an approximately 200 × 200 m grid of narrow research trails over the entire study area. A few main trails have narrow raised wooden boardwalks for part or all of their length in order to facilitate observers' travel efficiency. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates and adhered to the legal requirements of Indonesia.

Data Collection

Individual focal data were collected from 2003 to 2010 in accordance with standardized field methods [<http://www.aim.uzh.ch/Research/orangutannetwork/FieldGuidelines.html>], including activities and heights recorded at 2 min intervals [see also Dunkel et al., 2013; van Noordwijk et al., 2012]. Orangutans

observed to use the boardwalks were not scored as being on the ground. Location points were taken every half hour on a hand-drawn map that was later digitized (early years), or with a handheld Garmin GPSMAP 78 series GPS unit (later years). Both methods involve a certain amount of error (approximately ± 10 m), however, because of the large spatial scale in which orangutans move, as well as the nature of our questions, it is unlikely that this error measure has influenced our analysis.

Focal individuals could not always easily be followed without disturbing them once they were travelling on the ground through dense vegetation. Therefore, we included all focal activity data as long as the individual was followed for at least 3 hr, to reduce the bias in the data due to the focal being “lost” on the ground. However, we used all data covering at least a half hour to calculate the speed of movement during travel bouts and to assess space use.

In total, the dataset covers over 32,300 hr of focal observation on all age-sex classes of orangutans (plus an additional 5585 hr on pre-weaned offspring sampled together with their mothers) by an experienced team. In the current analyses, we distinguish between “immatures”—all weaned immatures, whether ranging in association with their mother or independently; “adolescent females”—ranging independently, sometimes sexually active, but nulliparous; “adult females”—all parous females (almost all accompanied by offspring); “unflanged males”—sexually mature males without cheek pads; “flanged males”—sexually mature males with fully developed secondary sexual features. In addition, some analyses were done on the dependent, pre-weaned offspring (infants) with known ages.

The monthly fruit abundance index was measured as the percentage of trees (in a phenology plot of over 1500 trees) bearing fruit [cf. Marshall et al., 2009]. Rainfall was measured daily at camp and minimum and maximum temperatures were measured daily at a fixed location in the forest, 50 m from the forest edge.

Twenty camera traps (Bushnell TrophyCam, 8 MP model) were installed throughout the study area, with at least 700 m between each one. The traps were active for a total of 3986 camera-trap days, between February 2010 and February 2012. The camera traps were programmed to take two photos, 10 seconds apart, whenever movement was detected. One “camera-trap record” refers to a set of two photos, and no camera-trap records of orangutans occurred at the same station on the same day, thus all records were considered independent. Fifteen of these cameras (3174 camera-trap days) were installed facing research trails at a height of 60–80 cm off the ground. The five additional cameras were located facing the raised boardwalks (812 camera trap days). All orangutan records ($N = 31$) were extracted and the age-sex classes of the orangutans in the photos were determined.

To control for possible observer effects, we analyzed changes in individuals’ time spent on the ground over the 7-year period, as the orangutans were presumably becoming increasingly habituated to observer presence. In order to control for observation biases due to losing focal orangutans prior to the end of a full-day follow, we totaled and compared the number of times that focal individuals were followed to their night nests, lost prior to building a night nest, and lost when they were moving on the ground prior to building a night nest.

Spatial Data Analysis

Exact locations were known for every instantaneous data point falling on the hour and the half hour, as well as morning, day, and night nests. Approximate locations were calculated for every activity data point (2 min interval), by equally distributing the distance between the nearest preceding and subsequent location points.

In order to investigate general ground-use spatial patterns, a grid cell analysis was first performed: all location points were overlaid onto a grid of cells measuring 200×200 m. Thus, the total time spent in each area (grid cell) could be compared with the time spent on the ground in each area. Second, all location points were overlaid with a map of the trail system and any points within 5 m of a trail were categorized as “on trail” (the 5 m buffer zone was included in order to accommodate mapping and GPS error). This allowed for a comparison of orangutans’ ground use on versus off trails.

Average travel speed was calculated for all follows lasting at least 3 hr by dividing the follow path length (measured between all subsequent half-hour points) by the duration of the follow. The overall travel speed during follows that did not include any movement on the ground were then compared to the overall travel speeds of follows which did include at least some movement on the ground. A second more detailed analysis of distance travelled during specific bouts of movement included data from any follow lasting at least 30 min, using the 2 min location points approximated between half-hour location points. A “travel bout” was defined as a 30 min period in which the individual’s activity was “Move” (locomotion in some way or other) during at least 10 (out of a maximum of 15) behavioral data points. Travel bouts began at the time and location of the first point where the point sample activity was “Move” and ended 30 min later, regardless of the temporal distribution of the 10+ “move points” during that time. If an orangutan continued to travel, and had at least 10 move points in the next 30 min, this was classified as a second travel bout. The distance traveled during these bouts was measured as the total distance travelled, from 2 min point to 2 min point, from the beginning to

the end of the 30 min. Travel bouts were then classified as having occurred entirely through the trees or as having included at least some ground travel, and the travel bout distances for the two groups were compared.

Statistical Analyses

All data were analyzed using χ^2 tests, Pearson's correlations, Kruskal–Wallis tests, and Wilcoxon signed-rank tests. For the Kruskal–Wallis and the time budget (activity and food items) Wilcoxon signed-rank tests, all data for each individual throughout the entire study period were summed, and individuals' scores were grouped by age-sex classes. For the kiss squeak analysis, as well as the average travel speed and the travel bout distance Wilcoxon signed-rank tests, each individual's mean scores were used, grouped by age-sex class where applicable (using median scores did not affect any of the conclusions). Thus, in order to avoid pseudo-replication in the data due to repeated sampling of the same individuals, each individual is represented by one data point in the analyses comparing time budgets, kiss squeak frequencies, travel distances, and speeds. Where simple statistical tests were not applicable, we have presented our results using descriptive statistics or as anecdotes. Camera-trap data are all described quantitatively, as were data investigating whether or not individuals' ground-use frequencies changed significantly over time as they became increasingly habituated to human observer presence.

RESULTS

Potential Biases and Habituation Effects

Long-term data consistently suggest that even habituated orangutans seem wary to descend to the ground when observers are present, and emit “kiss squeaks”—apparently toward observers—more frequently when they are close to or on their way to the ground than when they are higher up in the canopy. In order to analyze kiss squeak frequency without habituation level as a confounding factor, we used only data collected from 2006 to 2010, i.e. after 2–3 years of habituation, on the 7 most frequently encountered and thus, most habituated females. For each follow series lasting 5–10 days, the proportion of 2 min intervals when the focal was on or at <5 m from the ground and emitted a kiss squeak and the proportion of 2 min intervals when the focal was >5 m off the ground and emitted a kiss squeak was calculated. Even though observers always attempted to remain at a respectful distance, these females kiss squeaked significantly more often when they were <5 m above the ground than when they were >5 m above the ground (Wilcoxon signed-ranks test: $Z = 28$, $P < 0.05$, $N = 14$, $r = -0.54$).

We also looked for bias in the observational data due to terrestrial behavior. Focal individuals were “lost” before they made a night nest in 17% of all 3215 follows. This was most often because the focal individuals were on the ground and could not be followed through thick vegetation where visibility is low but following too closely would disturb them and human locomotion is necessarily slow ($N = 331$ times, or 60% of the lost cases). However, flanged males were much more frequently lost overall, and they were also twice as often lost while on the ground than females, immatures or unflanged males ($\chi^2 = 272.81$, $df = 4$, $P < 0.001$; see Fig. 1).

To examine whether focal orangutans gradually change their patterns of terrestriality in the presence of observers (i.e. long-term habituation effect), we compared the yearly proportion of ground use after 2–3 years of habituation, for four adult females for whom we had at least 200 hr of focal data per year during multiple years. Figure 2 shows that there was no consistent pattern in time spent on the ground as these individuals became increasingly familiar with human observer presence over the years. Thus, the observations of the well-habituated individuals provided relatively unbiased estimates of their natural ground use. However, we did not include data collected on unhabituated individuals, trying to flee or hide from observers or giving distress vocalizations for extended periods.

Frequency and Behavioral Correlates of Ground Use

Tuanan orangutans spent, on average, 2.29% of the total focal observation time on the ground. When including only those individuals for whom there is over 200 hr of data (total: $N = 25$; immatures: $N = 2$; adolescent females: $N = 2$; adult females: $N = 8$; unflanged males: $N = 6$; flanged males: $N = 7$), there is a significant difference between age-sex classes in the proportion of time spent on the ground

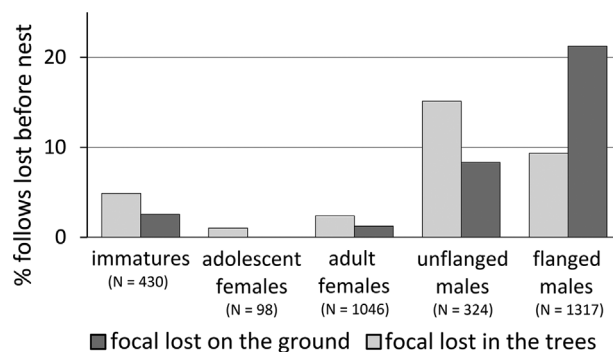


Fig. 1. The percentage of follows in which the focal individual was lost in the trees (light gray) and lost on the ground (dark gray) before making a night nest. The total number of focal follows started (either from morning nest or found during the day) is indicated per age-sex class.

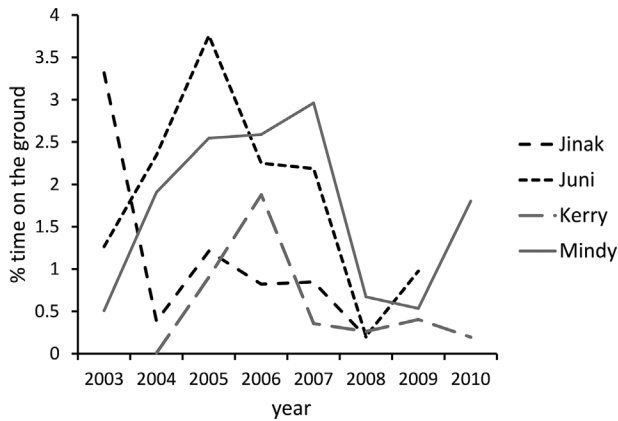


Fig. 2. The percentage of time spent on the ground by habituated females for whom >200 hr of focal data was available for at least 4 different years (all individuals, as well as the combined Pearson correlations are not significant, $P > 0.10$).

(Kruskal–Wallis test: $H(4) = 11.85$, $P < 0.05$) and post-hoc tests reveal that the only significant difference is between adult females and flanged males: flanged males spent significantly more time on the ground than did adult females (Fig. 3). Note, that other pairings' differences were likely not significant primarily because of the small number of included individuals in the immature ($N = 2$) and adolescent female ($N = 2$) age-sex classes.

When the study started in 2003, an adult female (Sumi) with a young offspring was found in the logged and burned area adjacent to the study forest. Since there were only a few (mostly dead) trees still standing in her presumed original home range, this female mostly foraged and moved on or close to the ground in the dense and low recovering vegetation (this also made it difficult to follow her without being too close, so the sample is likely an underestimate of her actual time on, or close to, the ground). Over the next three years, this female moved completely into the forested study area, where she spent only ca 1% of her time (close to the average for mothers with dependent offspring) on the ground vs. >12% of her time on average during her first full year of being studied. Thus, her initially high use of the ground was forced upon her by the circumstances, whereas she became more arboreal and avoided being on the ground again when she had the opportunity.

We also compared activity budgets and diet composition on the ground versus in the trees. This analysis only included individuals for whom we have at least 200 hr of data and who were observed to spend at least 1 hr on the ground (immatures: $N = 2$; adolescent females: $N = 2$; adult females: $N = 6$; unflanged males: $N = 6$; flanged males: $N = 7$). A comparison of focal individuals' activity budgets when on the ground versus in the trees (Fig. 4) shows that adolescent and adult females, as well as immatures, spent a greater proportion of time

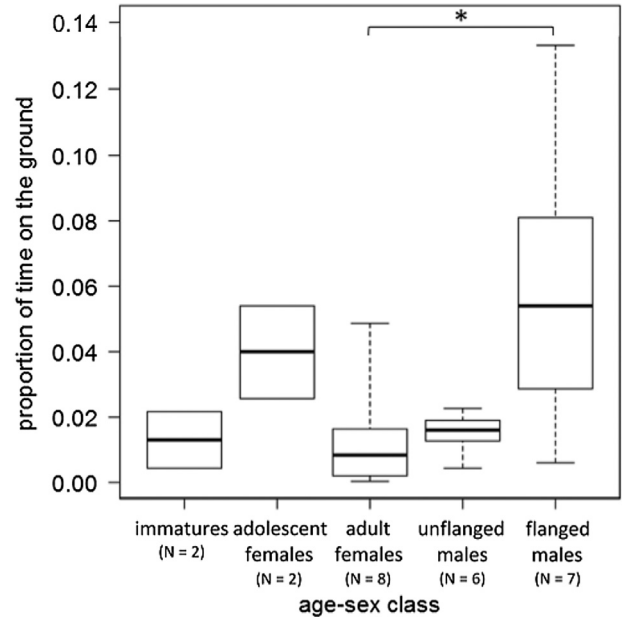


Fig. 3. The proportion of time during which individual habituated focal individuals were on the ground, by age-sex class. Center lines represent medians and whiskers extend to the maximum and minimum values of the data (* $P < 0.05$).

feeding and a smaller proportion of time resting when on the ground. Indeed, this difference was significant for adult females (Wilcoxon signed-ranks test: (feeding) $Z = 21$, $P < 0.05$, $N = 12$, $r = -0.62$; (resting) $Z = 21$, $P < 0.05$, $N = 12$, $r = -0.62$). Flanged males spent a greater proportion of time moving when on the ground (Wilcoxon signed-ranks test: $Z = 28$, $P < 0.05$, $N = 14$, $r = -0.65$), and reduced their proportion of time spent resting when on the ground (Wilcoxon signed-ranks test: $Z = 2$, $P < 0.05$, $N = 14$, $r = -0.53$). Unflanged males had the same activity profile in the trees and on the ground.

The diet composition of all age-sex classes while on the ground differed from that when up in the trees: all orangutans spent much more time feeding on insects, mostly termites, which are found in decaying wood (Fig. 5). This difference was significant for flanged and unflanged males (Wilcoxon signed rank tests: (flanged males) $Z = 28$, $P < 0.05$, $N = 14$, $r = -0.65$; (unflanged males) $Z = 21$, $P < 0.05$, $N = 12$, $r = -0.62$). In addition, all orangutans more often drank water while on the ground, even though water was sometimes also obtained from treeholes. Wilcoxon signed rank tests showed that this difference was significant for adult females ($Z = 21$, $P < 0.05$, $N = 12$, $r = -0.62$), flanged males ($Z = 27$, $P < 0.05$, $N = 14$, $r = -0.58$), and unflanged males ($Z = 21$, $P < 0.05$, $N = 12$, $r = -0.62$). With the exception of immatures, individuals also tended to spend more time feeding on vegetative plant parts (mostly mature leaves and stems for *Ficus* spp., pith of *Pandanus* spp. and *Zingiberaceae*) while on the ground, although this contrast was not significant for any age-sex class.

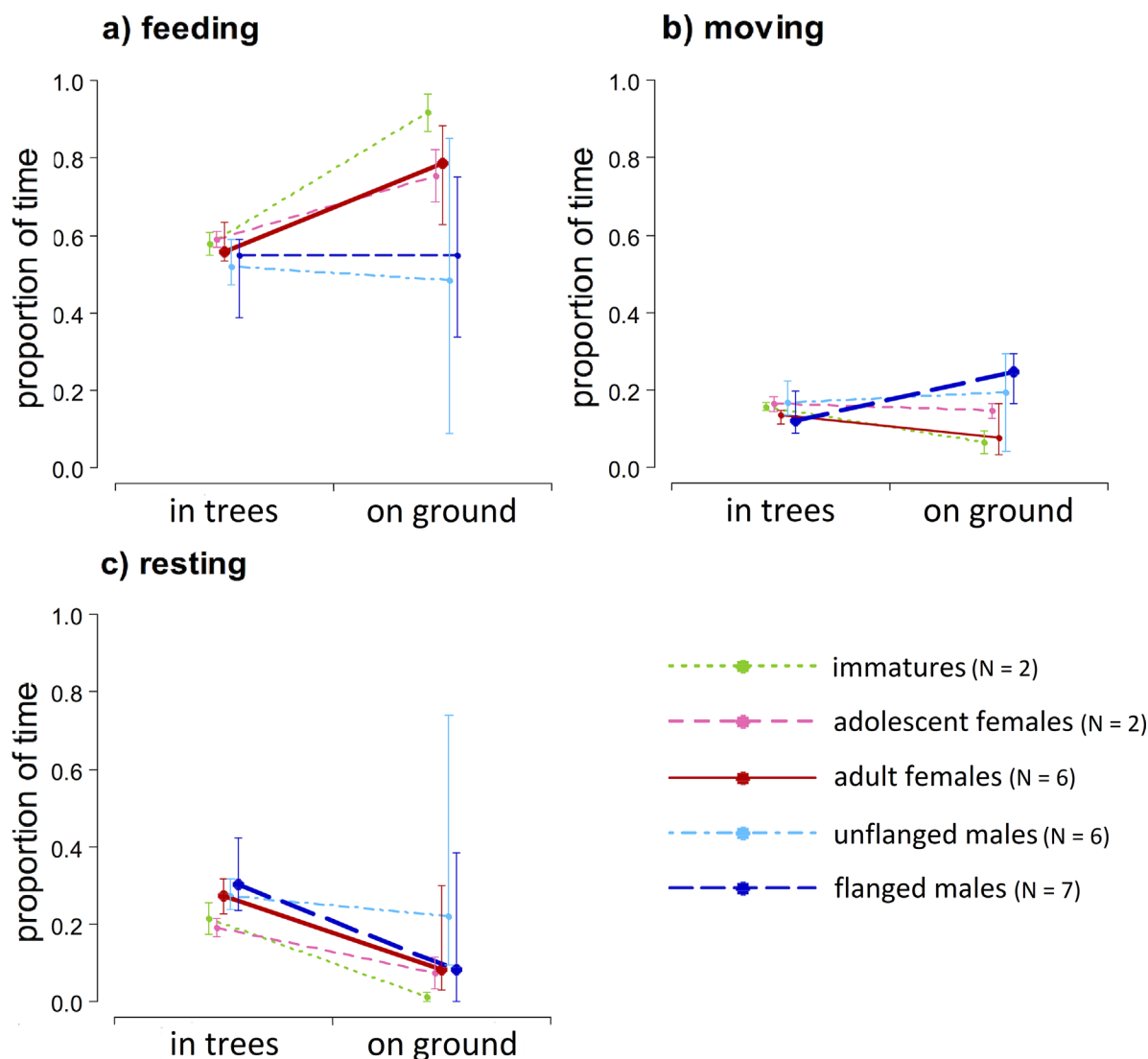


Fig. 4. The difference in proportion of time that focal individuals spent feeding (a), moving (b), and resting (c) while in the trees versus on the ground, by age-sex class. Proportion of time spent engaging in each activity is of the total proportion of time spent on that substrate (ground or trees). Thicker lines denote significant differences ($P < 0.05$).

It is important to note that most food items usually found on the ground can also be found in—or at least easily carried up into—the trees, and therefore do not actually require orangutans to stay on the ground during or after collection. Indeed, all food items except for termites, soil, and water, were more often consumed while in the trees than while on the ground, when considering absolute, rather than proportional, amount of time spent feeding on the items. Indeed, termites—which were the overall most-consumed food item while on the ground—were consumed more often in the trees than on the ground by all adult females, all unflanged males, one flanged male, all adolescent females, and all immatures. Water was more often drunk while in the trees than while on the ground by 2 adult females,

2 flanged males, 1 unflanged male, and 2 immatures. Of those individuals observed to consume soil ($N = 11$), 2 (both of whom were adult females) consumed it in the trees, rather than on the ground.

Mothers may be more likely than other adult age-sex classes to carry termite-infested logs up into the trees. Such “termite-logs” are often shared - that is, mothers tolerate and actively enable co-feeding by their offspring. Independently mobile offspring seemed reluctant to spend time on the ground and tended to stay behind in the trees, or climbed back up faster, when their mothers were on the ground. Figure 6 shows the proportion of time that a dependent offspring was on the ground when his/her mother was, and the proportion of time that a mother was on the ground when her dependent

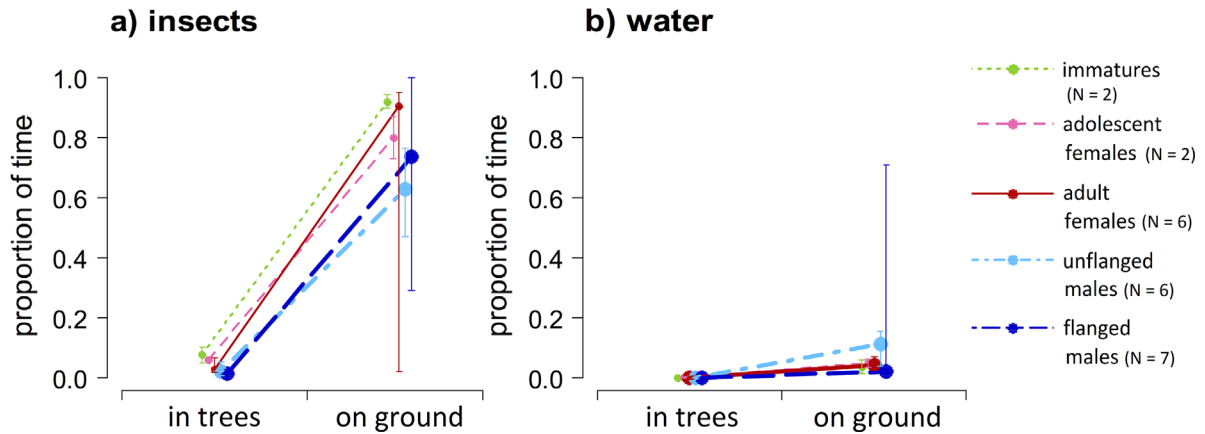


Fig. 5. The difference in proportion of time that focal individuals spent feeding on insects (a), and water (b), while in the trees versus on the ground, by age-sex class. Proportion of time spent feeding on each item is of the total proportion of time spent feeding while on that substrate (ground or trees). Thicker lines denote significant differences ($P < 0.05$).

offspring was, broken down by age of the offspring. As offspring matured, they were increasingly likely to follow less closely and stay up in the trees when their mothers descended to the ground, and offspring were hardly ever on the ground without their mothers until they were at least 5 years old. In addition, even though it seems much easier for a small infant to move around on the ground than in the trees, dependent immatures up to age of 4–5 years were consistently more likely to be clinging to their mothers while on the ground than while in the trees during maternal moving, feeding and resting (Fig. 7).

In contrast, some social conditions seem to encourage leaving the trees. Orangutans fleeing from conspecifics, either in response to an agonistic encounter or as a form of preventive distancing, sometimes choose to descend to the ground and then quickly move away: in 44% (28 out of 62) of observed events of fleeing, the fleeing individual did so on the ground (Fig. 8).

After an individual fled from a conspecific on the ground, the association (proximity within 50 m) ended in 96% of the 28 cases, compared to only 68% of the 34 events when an individual fled through the trees ($\chi^2 = 6.71$ Yates corr, $df = 1$, $P < 0.01$). Furthermore, during her first years in the study area, the above-mentioned female, Sumi, disappeared over the ground whenever she encountered another orangutan, especially one of the resident females.

Environmental Correlates of Ground Use

Monthly rainfall in the Tuanan swamp forest is highly variable within and between years [van Noordwijk et al., 2013]. On average, the least rain falls in August and September (<100 mm/month) and the most rain falls in December to April (>300 mm/month). However, there was no relationship between the amount of rain in the previous 60 days or 30 days (intended as a proxy measure for

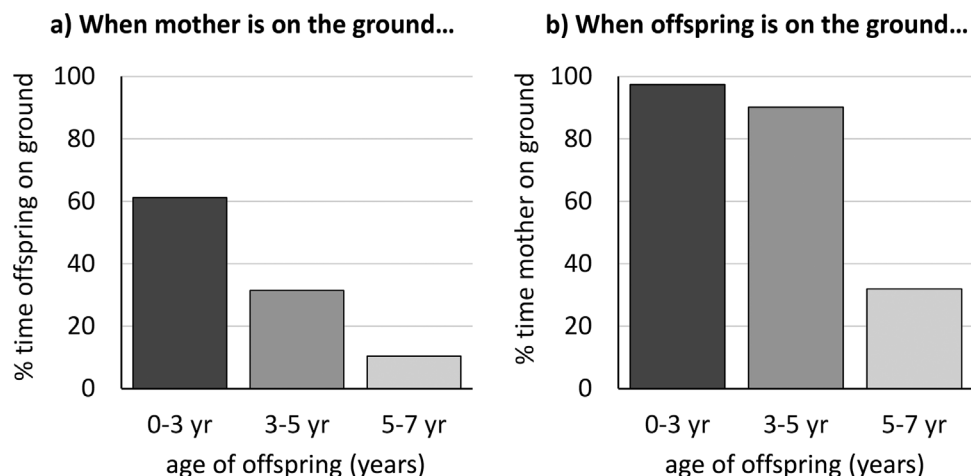


Fig. 6. The percentage of time that a dependent offspring was on the ground while his/her mother was on the ground (a), and the percentage of time that a mother was on the ground when her dependent offspring was on the ground (b), by offspring age class.

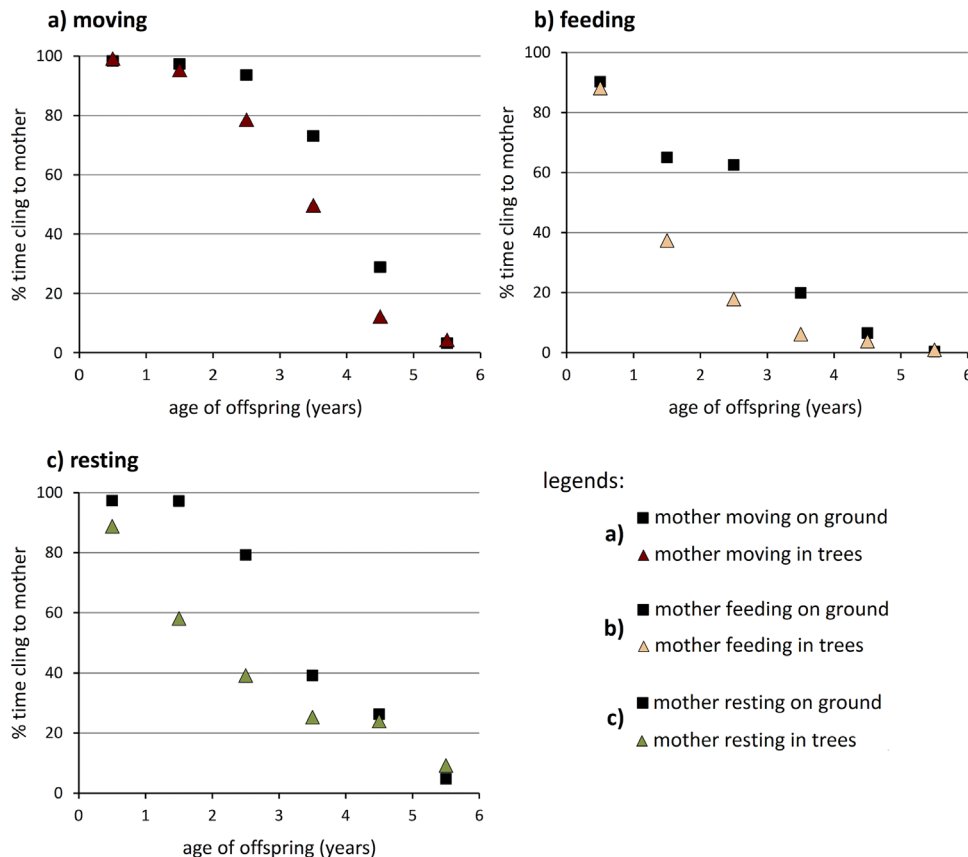


Fig. 7. A comparison of the percentage of time that a dependent offspring was clinging to his/her mother during moving (a), feeding (b), and eating (c), while his/her mother was on the ground versus while she was in the trees, by offspring age.

standing water) with the proportion of time individuals spent on the ground per focal follow ($N = 3428$ days, $N = 3456$ days, respectively).

Average monthly maximum temperature in the forest (28.8°C) varied little (range of monthly average: 28.1°C in January to 29.5°C in September). Focal individuals were occasionally seen standing or sitting in standing water on the ground, splashing themselves or even rubbing themselves with wet leaves. In total, 14 different individuals representing

all age-sex classes were observed to do this at least once. Even though these individuals seemed to cool off this way, the maximum temperature (measured at a fixed location) was barely higher on days with this “bathing” behavior than on days without it (average during focal follows with “bathing” $T_{\text{max}} 29.10 \pm \text{SD } 1.64^{\circ}\text{C}$, $N = 32$ versus average during focal follows without “bathing” $T_{\text{max}} 28.72 \pm \text{SD } 1.58^{\circ}\text{C}$, $N = 3706$) and well within the measuring error of our thermometers. Thus, although many different Tuanan orangutans seem to use standing water for apparent comfort behavior, the frequency of this is very low (at least in the presence of observers) and not clearly related to weather conditions.

During periods of food scarcity, orangutans may be expected to increase their time spent on the ground, either in order to collect fallback foods or to save energy by travelling longer distances over the ground. However, there was no consistent effect of fruit availability on the proportion of time that individuals spent on the ground, using the averages per age-sex class (based on at least 50 hr) per month. Adolescent females (the age-sex class with the smallest sample) are the only age-sex class to show a significant correlation. However, it is in a direction opposite to the expected one: as fruit availability

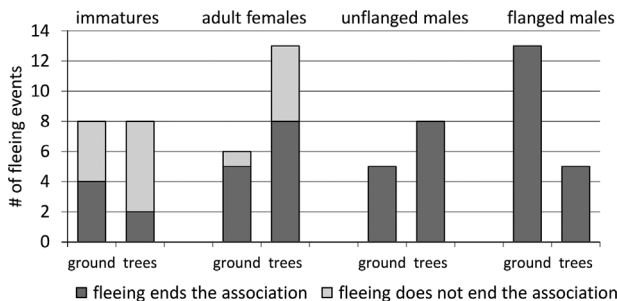


Fig. 8. The number of observed fleeing events (from conspecifics) through the trees and on the ground, comparing cases that did not result in the termination of the association (distance between conspecifics remained within 50 m) (light gray) and those that did end the association (dark gray).

increased, the time they spent on the ground also increased (Pearson's $r = 0.695$, $N = 12$ month samples of ≥ 50 hr, $P < 0.05$). Most age-sex classes with larger samples (including immatures, unflanged, and flanged males) showed the expected negative trends, as did lumping all class samples together, but all these were non-significant, (Pearson's $r = -0.080$, $N = 198$ month samples, $P > 0.10$).

Spatial Distribution of Ground Use, and Speed of Ground Travel

Orangutans spent time on the ground in all parts of the study area, and overall, did not favour ground use in particular areas. There was a positive correlation between the total number of location recordings and the number of on-the-ground location recordings in each grid cell of the study area (Pearson's $r = 0.69$, $N = 282$, $P < 0.001$). There were two noticeable outliers—grid cells in which orangutans spent more time than expected on the ground. In these cells (which are adjacent), orangutans spent a relatively high proportion of time feeding on termites (66.2%, 84.5%). This suggests that the spatial distribution of termites has a large influence on the spatial distribution of orangutan ground use.

Overall, orangutans were within 5 m of a research trail in 8.4% of all on-the-ground observations, and in 9.0% of all above-ground observations. Flanged males were occasionally observed to move on the ground along trails; however, there were no significant differences between ground use on and off trails for flanged males or any other age-sex class, except for independent immatures, who were significantly less likely than expected to be on a trail when on the ground ($\chi^2 = 4.79$, $df = 1$, $P < 0.05$).

Among flanged males, the overall speed of travel during follows of at least 3 hr which did not include any ground travel was significantly lower than for those which did include at least some ground travel (Wilcoxon signed-rank test: $Z = 10$, $P < 0.005$, $N = 32$, $r = -0.57$). Furthermore, among flanged males, the distance travelled during 30 min travel bouts was significantly farther during bouts that did include some ground travel than bouts which took place entirely through the trees (Wilcoxon signed-rank test: $Z = 21$, $P < 0.05$, $N = 12$, $r = -0.62$) (Fig. 9). It is important to note, however, that even the distances travelled by flanged males during 30 min travel bouts that took place entirely on the ground (no travel through the trees at all) ($N = 3$, range = 97–498 m) do not exclusively exceed the maximum distance travelled by a flanged male during a 30 min move bout taking place entirely through the trees (428 m). No other significant relationships between speed or distance travelled and movement on the ground were found for any age-sex class, over entire follows or during specific travel bouts.

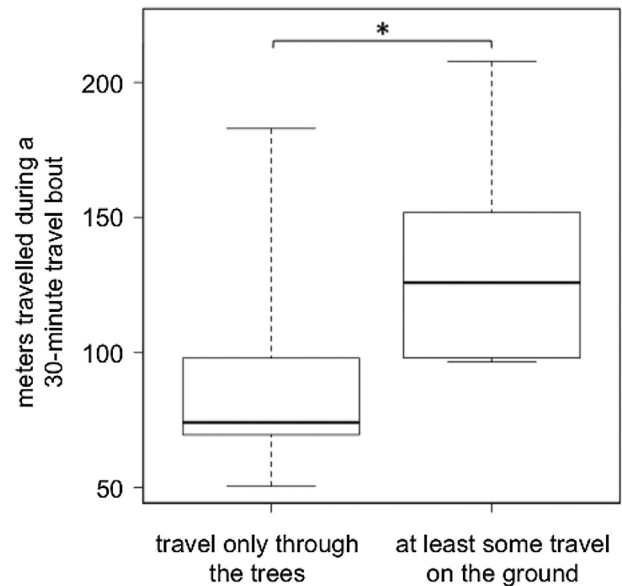


Fig. 9. The difference in distances travelled during 30-min travel bouts which occurred entirely through the trees versus those which included some ground use, for flanged males only ($N = 6$). Center lines represent medians and whiskers extend to the maximum and minimum values of the data (* $P < 0.05$).

Evidence of Orangutan Ground Use From Camera Traps in Tuanan

Within the study area, orangutans were photographed by ground-level camera traps 19 times (on average 0.006 times per trap day). Over half (53%) of the Tuanan camera-trap records were of flanged males, while the age-sex classes of 8 orangutans in the remaining records (47%) could not be reliably determined, although, all were at least adolescent size and 4 were definitely not flanged males. This means that flanged males were recorded in a minimum of 53% and maximum of 77% of camera-trap records. The additional 5 camera traps directed at raised boardwalks recorded females with offspring at least 3 times and flanged males 7 times, out of a total of 12 records—for 0.015 records per trap day. Orangutans were significantly more likely to be recorded by camera traps facing the boardwalks than by those facing the trails ($\chi^2 = 5.39$, $df = 1$, $P < 0.05$).

DISCUSSION

Reasons for Ground Use in Tuanan

Although, until now, behavioral studies of wild Bornean orangutans have only reported terrestriality anecdotally, it is clear that ground use is within their natural behavioral repertoire. Consistent with early reports from other studies [e.g. Galdikas, 1979; MacKinnon, 1974], flanged male orangutans at Tuanan spent more time on the ground than any other age-sex class. Indeed, we found that flanged males were the most often lost age-sex class by

observers, often because they would descend to the ground, and thus our estimate of ground-use rate for flanged males is likely biased towards an underestimation. Furthermore, while flanged males often traveled along the ground, adult females primarily came to the ground to feed on certain resources, such as termites. We found no evidence of a strong spatial bias to orangutan ground use, except that orangutans forced to live in more open areas spent much time on the ground. Instead, orangutans did spend more time than expected on the ground where they could most often engage in termite feeding. Thus, ground use is not simply a response to canopy gaps or unsuitable habitat [cf. Ancrenaz et al., 2014], but occurs to satisfy specific needs.

Orangutans at Tuanan were observed to descend to the ground to collect, and sometimes consume, food items, including termites, water, and peat-soil/turf. In the homogenous peat-swamp forest at Tuanan, standing water is available and consumed throughout the study area, and there is no indication that it satisfies any nutritional/mineral needs aside from thirst (in contrast to drinking from salt lick pools as described for some other sites e.g. Matsubayashi et al. [2011]).

There is nonetheless strong evidence for an innate wariness of the ground. First, resting on the ground was extremely uncommon for orangutans other than flanged males. Second, even the most habituated adult female orangutans were more likely to kiss squeak when they are on their way to, or already on, the ground. Kiss squeaks are interpreted as both alarm and mobbing calls [Hardus et al., 2009] and alert others (mostly offspring) to watch out, but also warn potential predators (including human observers) that they have been noticed and will be chased if they come too close (Tuanan unpublished observations on humans and a dog). Lastly, small (unweaned) immature orangutans hardly ever descended to the ground alone, and even only rarely accompanied their mothers down to the ground, unless they could cling to her body. This apparent reluctance of small immatures to spend time on the ground, even when their mothers do, may explain why adult females did not spend significantly more time feeding on termites on the ground than up in the trees, while adult males, both flanged and unflanged, did. Thus, mothers may spend less time on the ground than would be efficient for themselves, to accommodate the needs of their young offspring. Indeed, adult females with dependent offspring are often observed to descend to the ground alone, and then carry a termite-infested log back up into the trees. These termites are then consumed in the canopy, where the offspring is allowed to co-feed.

The camera-trap data confirmed these observational findings. Immatures avoid coming to the ground on trails, supporting the notion that they only leave the trees when the attraction, i.e. feeding

opportunity, is strong enough and not to travel or cross canopy gaps. Adult females with dependent offspring were recorded relatively more frequently on raised boardwalks than on trails, suggesting mothers with offspring avoided travelling on the ground when possible.

This pattern suggests that there may be a learned loss of fear over the course of an individual's life: as a young orangutan increasingly often accompanies its mother to the ground, grows in body size, and becomes more familiar with ground-based resources such as termites, terrestriality becomes a more regular component of its behavioral repertoire and its natural aversion to ground use is lessened. This indicates that regular ground use among Bornean orangutans may be a relatively recent addition to their behavioral repertoire, perhaps only since the extinction of tigers on the island (which may have occurred as recently as the early Holocene [Kitchener & Dugmore, 2000; Louys, 2014; Piper et al., 2007]). These learned behaviors have served to increase the feeding niche of all, as well as the mobility of male, orangutans.

This interpretation is bolstered by the fact that Bornean orangutans do not show obvious anatomical differences compared to their Sumatran counterparts, and thus lack any clear adaptation for terrestrial locomotion, such as the knuckle-walking capabilities of chimpanzees and gorillas. Indeed, since splitting from the common hominid ancestor, it is likely that orangutans' adaptations to arboreality have been further refined [Thorpe and Crompton, 2006].

Sumatran orangutans still share their range with tigers, and indeed rarely descend to the ground, except in social emergencies or to collect food and quickly carry it up into the trees [Rijksen, 1978; van Schaik, 2004; in the swamp forest of Suaq Balimbing habituated females spent <0.05% on the ground and even flanged males were <0.25% terrestrial: C. Schuppli, personal communication]. However, for both species, other predators such as clouded leopards, snakes, and wild pigs, are a potential threat to especially the smaller-bodied individuals, explaining their wariness to be on the ground (see Kanamori et al. [2012] for an example of a predation event on a juvenile orangutan). This wariness is less obvious among the large-bodied, and thus less vulnerable, flanged males, who even occasionally spend nights on the ground in Tuanan. Indeed, ground nesting by flanged males at Tuanan was observed 3 times during the study period ($N=442$ follows to nest), but has been observed more frequently since (in the period of 2010–2012: 10 out of 197 follows to nest), with one male accounting for 9 of those nights. Individuals of other age-sex classes were never observed to nest on the ground, with the exception of the adult female whose home range was burned—she was observed to spend at least 4 nights

on the ground when she was still ranging in her original home range after it had been cleared (i.e. before she began to push her range into the adjacent forested area). Thus, the only individuals who ever nested (apparently) voluntarily on the ground were large-bodied flanged males.

Over the course of several hours, or even full days, flanged males travel faster when a proportion of their movement occurs on the ground. This is not seen for other age-sex classes, which may be because their terrestrial movement is often done in the context of searching for food and may therefore be much less unidirectional than that of larger males who are using the ground more for travel without inspecting foraging options. Because location points were only recorded every half-hour, the sinuosity of individuals moving around and searching for food on the ground was not measured. Interestingly, only 4% of adult females' 30 min travel bouts included any ground-travel (as compared to 22% for flanged males), showing that when adult females are engaging in relatively consistent movement (rather than that which is heavily interspersed with feeding, for example), they rarely include any ground travel.

Our analysis of distances traveled during 30 min travel bouts shows that flanged male orangutans are able to move quickly both on and off the ground but that there is an association between including at least some terrestrial locomotion and higher speeds. However, because flanged males travelling only through the trees were often able to reach travel speeds as fast or nearly as fast as those incorporating some ground-use, it is likely that factors other than simply the potential speed of travel have a large influence over whether or not an individual moves on the ground or in the canopy.

Although, Bornean orangutans do not show specific morphological adaptations for terrestrial locomotion, there is evidence that they are able to move relatively inconspicuously—even when moving quickly—along the ground. First of all, the relatively high rate at which focal individuals are lost by observers when on the ground, compared to when in the trees, demonstrates that it is much harder for humans to follow an orangutan who is moving along the ground than one who is moving through the trees. At Tuanan, orangutans on the ground hardly disturb or rustle the thick undergrowth when moving, the way that they disturb the trees when moving through the canopy. Thus, even a small distance of 5–10 m between the focal orangutan and its observers is often enough for observers to lose sight of the orangutan entirely.

Secondly, there is evidence that losing contact with an orangutan who is moving on the ground may not be only a human problem: orangutans fleeing from conspecifics on the ground were more likely to end the association than those fleeing through the

trees. Thus, at least at Tuanan—where the forest is mostly made up of small, pliable trees—fleeing over the ground may be a more effective strategy to end unwanted associations with conspecifics than fleeing through the trees, which involves noisy and conspicuous movements such as tree swaying. This all indicates that in some closed canopy forests, orangutans' travel along the ground can be less conspicuous than travel through the trees, and social factors may greatly influence whether or not an orangutan chooses to travel on the ground. In Borneo, where competition between orangutan males can frequently turn violent [Dunkel et al., 2013], it is not surprising that males often seem to attempt to move around undetected by conspecifics.

Another common hypothesis to explain ground travel over longer distances by orangutans is based on the assumption that travel on the ground is more energy-efficient than through the trees, which may require frequent directional diversions in all three dimensions [Cant, 1987]. This would especially be true where canopy structure and connectivity are poor. Saving energy by moving along the ground could be especially beneficial for the large-bodied flanged males, and thus explain why they are the most likely age-sex class to move on the ground and why this ground-movement is associated with higher speeds and travel over longer distances. It has been suggested that microclimate might be an additional advantage of ground travel, e.g. Takemoto [2004] found that chimpanzees spent more time on the ground during the dry season and speculated that this helped them to stay cool and thus reduced their metabolic costs associated with thermoregulation. Measurements at Tuanan [Hermann, 2010] have shown that maximum temperature tends to be higher at the mid-canopy level (5 m or 10 m) than closer to the ground. It could therefore be speculated that, at least in the case of long-distance ground travel by the larger-bodied males, ground use increases when canopy temperature increases. However, the general patterns of ground use among Tuanan orangutans do not show a meaningful relationship with daily maximum temperature (measured at approximately 1.3 m off the ground). Furthermore, standing swamp water is also often used for bathing. Despite this behavior seeming to cool the orangutans off, it did not specifically occur on especially hot days. Thus, it is still unclear to what extent ground travel (and use in general) aids orangutans in reducing thermoregulatory costs.

One other potential explanation for ground travel, especially for the large-bodied males, is that it may reduce their risk of falling. Orangutans at Tuanan are occasionally observed to fall—either all the way from the canopy to the ground, or within the canopy from higher up to lower down—when supports break under their weight. Evidence of long bone fractures consistent with falls out of the

forest canopy has been found among great apes, including orangutans [Kehoe & Chan, 1986; Kraft et al., 2014]. This risk of injury from falling may be especially high for the heaviest orangutans, the flanged males, and thus may contribute to their more frequent ground travel.

Comparison With Other Sites

Our camera-trap data show that the frequency of orangutan terrestriality at Tuanan falls within the range of ground-use frequencies reported from other sites in Borneo [Ancrenaz et al., 2014]. Of all the camera-trap study sites, Tuanan is perhaps most comparable with the Sabangau study site, in terms of forest type (peat-swamp forest) and current and past management classification (“old and slightly logged forest”), as per Ancrenaz et al. [2014]. Orangutan density at Tuanan is approximately 3 times higher than at Sabangau, and the total camera-trap rate of capture at Tuanan is 3 times higher than at Sabangau. This suggests that orangutans in these two similar forests may be spending comparable amounts of time on the ground.

Interestingly, the rate of camera-trap captures of orangutans on the ground from the dryland, formerly selectively logged area in Wehea Forest [Loken et al., 2013, breakdown of counts reported in Ancrenaz et al., 2014] is almost twice that of Tuanan, despite an orangutan population that is 4 times less dense. This suggests that the orangutans (*P. p. morio*) living in Wehea Forest spend far more time on the ground than the orangutans (*P. p. wurmbii*) of Tuanan. Furthermore, the camera-trap study of Loken et al. [2015] demonstrates a propensity for ground use among various age-sex classes of orangutans, including adult females with and without dependent offspring. Indeed, in all 3 forest types, adult females accounted for 41% of camera-trap records, while flanged males accounted for 23–36% of records [Loken et al., 2015]. This suggests that in the areas studied by Loken et al. [2013, 2015], ground use by age-sex class may be different than among the Tuanan orangutans. Unfortunately, it is not yet possible to determine the relative contribution of structural factors (forest type, canopy structure, etc.), population/sub-species differences, or other factors, to this substantial observed difference. We suspect that food availability and distribution does play a role at this between-population scale.

In conclusion, we have shown that terrestriality is a normal component of the Bornean orangutan behavioral repertoire. In Bornean forests, even those with a relatively closed canopy, orangutans occasionally descend to the ground in response to unwanted associations, to retrieve attractive food sources (some of which, e.g. termite logs, may be carried up into the trees), and—especially in the

case of flanged males—to travel. However, like Sumatran orangutans, Bornean orangutans do appear to have an innate fear of the ground. Unlike Sumatran orangutans, though, they gradually overcome this fear during ontogeny, although females never do so completely. The proportion of time spent on the ground differs between individuals and between populations, but for now the role of food scarcity, canopy structure, or other factors remains unclear.

The tendency of Bornean orangutans to come to the ground may better equip them to deal with forest degradation. In this respect, the Bornean orangutan may have more behavioral flexibility as to habitat use than Sumatran orangutans. This difference may enable Bornean orangutans to better cope in disturbed, fragmented, and human-dominated landscapes.

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